COMPARATIVE

SENSORY & COGNITIVE

ADAPTATIONS FOR

EXPLORATORY LEARNING

IN PARROTS & HUMANS

by

ZOE P. DEMERY

A thesis submitted to the University of Birmingham for the degree of
DOCTOR OF PHILOSOPHY

supervised by Dr. Jackie Chappell

Cognitive Adaptations Research Group
School of Biosciences
College of Life & Environmental Sciences
University of Birmingham
September 2012

ABSTRACT

How do different animals cope with the vast environmental complexity they face from birth or hatching? If animals' genes have not provided the necessary information, then exploration is essential for gathering information and learning about the surrounding world. Much of cognition research to date has focussed on what the different abilities of different animal species are, rather than how they actually process information. This thesis has taken a distinctive interdisciplinary approach to tackle this problem from different angles: asking how the senses, environment and different behavioural strategies influence exploratory learning – specifically in the naturally exploratory parrot and human child. It investigated parrots' visual fields and their tactile 'bill tip organ' to describe the limits of their sensorimotor exploration, both in approach to and during manipulation of an object. A series of increasingly complex behavioural tasks were also conducted with parrots and children, involving different novel objects and causal problems. This project has given us insight into how we and other animals structure information in different situations. It has the potential to expand the understanding of a wide range of fields, such as in aiding how human developmental disorders may be treated, or by informing robotics design.

c.

"She was not quite what you would call refined. She was not quite what you would call unrefined. She was the kind of person that keeps a parrot."

MARK TWAIN

For my cognitively-challenged muse, Bella, and for parrot lovers everywhere, but especially for the wonderful people by their side who put up with them.

Acknowledgements

There is not enough space to express just how much gratitude I feel towards all of the numerous people who have made this thesis possible – but I'll try anyway!

First and foremost, Jackie Chappell – I could not have asked for a better supervisor. Your patience and support knows no bounds. Your exuberance in the face of all challenges, not to mention your unique take on animal learning has greatly inspired me. Thank you.

I owe my deepest gratitude to Susannah Thorpe and Claudia Mettke-Hofmann, my examiners. Susannah has provided valuable advice and encouraged me to pursue novel angles from day one of my Ph.D. Claudia very kindly agreed to take on this mammoth task although I sprung it upon her without much notice. I hope you both enjoy the read! Thank you.

I have been very privileged to collaborate with wonderful individuals from a range of disciplines. In particular on the sensorimotor side, Graham Martin: your enthusiasm is infectious – you've opened up a whole new world to me. Thank you. From the developmental psychology side, Sarah Beck: always happy to involve me in a multitude of things; you gave a once hard-core behaviourist a fresh outlook on the wonders of the mind. Thank you. Last, but certainly not least, the cognitive roboticists, Vero Arriola-Rios and Aaron Sloman: you admirably indulged a complete computing newbie, but gosh what fascinating discussions we've had – I hope they don't stop. Thank you.

The interdisciplinary work didn't end with them though. I am indebted to the rest of the Cognitive Developmental Research Group in the School of Psychology, especially Ian Apperly and Nicola Cutting. Also to the rest of the Intelligent Robotics Lab in the School of Computer Sciences, principally Jeremy Wyatt, Nick Hawes and Rustam Stolkin. Thank you.

My colleagues within our own lab group have provided me with abundant support, both of the technical, intellectual kind and otherwise! Jolyon Troscianko, Emma Tecwyn and Abi Phillips – thank you. Katy Jones and Roland Brandstaetter provided valuable histological advice, when a behavioural zoologist did not mix so well in the lab – thank you. Simone Webber kindly translated key (though what seemed to be ancient!) French papers for

me – thank you. Kirsten Manduell was there from the beginning and kept me sane with a wee tipple when I most needed it – thank you. The rest of the office gals (and boys) were simply awesome: Kaat Brulez, Camille Duval, Julia Myatt, Jen Smith, Shivani Singh, Kiran, James, Gisela Helfer and Tim Harrison – thank you. Leigh Nash, Tony Kelly and the rest of the Chaddesley Ringing Group welcomed me to a different but fun side of ornithology (even if I do put in the poles backwards or scribe far too slowly) – thank you. The SyMoN group, especially Alan Wing, Dagmar Fraser, Nick Roach and Rachel Wright, for the brainstorming sessions on parrot grip and haptic exploration – thank you. Also to everyone else from the corridor, Biosci and GEES for making my Ph.D. what it was (you know who you are!) – thank you.

Special mention needs to go to Pete Jones and Phil Archer, not only for looking after all those pesky psittacines, but also for building me odd bits and pieces, actually partaking in some of my experiments, allegedly not minding me contacting them at all hours, and simply for being there when it seemed like I hadn't seen another human being for days. Thank you. I am also indebted to all the Biosci workshop guys, who were ever tolerant of my rubbish drawings and attempts to explain my latest 'scientific' ideas, which were essentially just elaborate toys. Thank you.

All of the human exploration work could not happened without the generous support of Jack-in-the-Box Nursery, Little Hippos Nursery and Nelson Junior and Infant School here in Birmingham. Thank you. The National History Museum at Tring, especially with the kind assistance of Jo Cooper, gave me access to their psittacine skeleton collection, which was most illuminating. Thank you. I also cannot forget the open-source community for providing me with so many fantastic free programs – they made my project a thousand times easier. Thank you.

I would not have become so captivated with the field if I had not been under the great tutelage of Arthur Goldsmith, Innes Cuthill, Tom Troscianko and Norman Freeman in Bristol. Thank you. I have hugely enjoyed many stimulating discussions and received very helpful advice about a range of issues (in no particular order) from: Jussy Gajdon, Murray Shanahan, Andrew Simpson, Greta Defeyter, Kim Bard, Sally Boysen, Mark Fletcher, Steve Spooner, Mike Land, Jessica Yorzinski, Sue Cunningham, Martin Wild and Lesley Rogers. Thank you.

I extremely appreciate all the enthusiasm I have been on the other end of from all kinds of people. A great many individuals volunteered their pets for me, in particular: Nicola Dennis, Sophie Webster, Paula Biddlestone, Jackson Kirkman-Brown, Janice Saul, Paul Bradley, Richard Clay, and Kathryn Matthews. Moreover, all the project and summer students – Ben Draper, Benedict Ludkin, Emma Poynter, Fraser Henderson, Gabrielle Sumray, James Boswell, Kate Vickers, Lauren Gripton, Charlotte James, Adam Farr, Gregory Dash, Eleanor Rhodes, and Thomas Hodson-Cottingham. Thank you.

This thesis would not have been possible without the financial support of

the Biotechnology and Biological Sciences Research Council and the British taxpayers. Thank you.

The unequivocal support of all my family and friends has been outstanding. Thank you for putting up with all the long silences when the parrots were keeping me busy. Thank you for always being there when I needed you. Thank you for all the encouragement and counsel that kept me going. In particular Roz Ellis and James Perrott: you have both been magnificent – words cannot express, but thank you. My sister, Lucy – you remain an inspiration to me to keep reaching for the stars. Thank you. My parents, Nigel and Valerie – I would not have got where I have today without you. At a loss for words for what all you have done means to me. Thank you.

Above all, my amazing husband, Christopher. I am so so so lucky to have found you. You have been my rock through all times. The sacrifices you've made for me are too many to mention, but without them this thesis would have remained a dream. I love you. Thank you.

Contents Overview

NB: Whenever a ⋆ appears next to a word or phrase, please see the Glossary (from page 344) at the back for a definition or some examples.

Detailed Contents

List of Figures

List of Tables

CHAPTER 1

Introduction

How do different species cope with the vast environmental complexity they face from birth or hatching? For species living in simple environments, their genes contain all the information[⋆1] they need to survive, so they are merely acted on by the environment. For species in more complex environments, they have evolved flexible cognitive and learning mechanisms, so they can gather information for themselves by acting on and altering the environment in some way. Since the time of Aristotle, biologists, psychologists and philosophers alike have deliberated over how individuals learn about the world around them. Exploration may play a key role.

Exploratory behaviour is itself a puzzling phenomenon: it is a seemingly random activity, which is energetically costly, and yet has no apparent function (Bekoff and Byers, 1998). However, exploration is frequently observed

[1] As exploratory learning covers many different fields, a glossary is provided (from page 344), with included terms denoted by a ⋆ symbol.

across the animal kingdom (Berlyne, 1960; Glickman and Sroges, 1966). The field is hampered by the lack of any useful or accepted definition (Power, 2000). Nonetheless, few now refute that exploration is fundamental for gathering information and for learning about the physical and causal properties of the world around us (Archer and Birke, 1983). For the sake of simplicity, exploration (or 'exploratory learning'*) is defined in this thesis as:

> ...any perceptual or motor interaction with objects, with no immediate benefit/function, except to gather environmental information, sometimes in parallel with another activity, including problem solving by goal-directed action.

By observing different species exploring different environments, we can gain a valuable insight into the underlying learning mechanisms and problem-solving strategies. Such an understanding has far-reaching implications, from treating human developmental disorders (both learning and motoric; e.g. Switzky et al., 1979), to designing intelligent robots (e.g. Hawes et al., 2010). Four broad theories about exploration have arisen from various disciplines.

Firstly, from the discipline of behavioural ecology, the information primacy model (e.g. Miller and Dollard, 1941; Harlow et al., 1950; Toates, 1983; Inglis, 1983; Greenberg and Mettke-Hofmann, 2001) proposes that information is a primary, intrinsic motivation (like hunger or thirst) for dealing effectively with the environment. Inglis and Langton (2006) described a model of exploring animals responding to environmental variability and concluded the key driver is uncertainty-reduction, trading-off with other 'need states'. The authors distinguished exploration from 'goal-directed behaviours'* like

foraging, which they argue guides exploratory behaviours. Others recently viewed exploration in an evolutionary context, acting in parallel with other motivations; neophilia* and neophobia*. Risky environments increase 'information value', but exploration only occurs when the benefits outweigh the costs (e.g. Gould, 1974; Greenberg and Mettke-Hofmann, 2001). However, these models do not focus on the cognitive processes interacting with these motivations, except in considering internal spatial maps (e.g. rats learning different routes through mazes; Toates, 1983; Rheingold, 1985; Loewenstein, 1994; Wemelsfelder and Birke, 1997), or how neural networks may reward an exploring animal (e.g. Redgrave and Gurney, 2006; Bunzeck et al., 2010). Taking an ecological standpoint, these researchers do not focus on the individual's perspective.

Secondly, from the field of animal cognition, the dichotomous learning model (e.g. Rescorla, 1968; Haselgrove, 2010) invokes learning mechanisms to explain various animal behaviours, which are termed either 'simple' or 'complex'. The simple mechanisms involve 'associative learning'*: the internal pairing of events in close temporal or spatial contiguity for detecting cause and effect (e.g. Seligman, 1970; Dickinson, 2012). Conversely, complex mechanisms (i.e. 'causal reasoning'*) require a flexible, abstract understanding of physics to solve causal problems (e.g. Visalberghi and Tomasello, 1998; Taylor et al., 2009a). Various species have been shown to have impressive cognitive capacities, previously thought to be unique to humans (e.g. Seed and Call, 2008; Byrne and Bates, 2011; Chittka and Jensen, 2011). However, rich detail is often missed by taking this dichotomous approach, and few have considered how animals gather and process information.

Thirdly, there is the hypothesis-testing model (e.g. Karmiloff-Smith and Inhelder, 1975; Tenenbaum, 1999; Rochat, 2001; Gopnik and Schulz, 2004; Legare, 2012) from developmental psychology, the source of most research about exploration. It is widely accepted that children 'learn by doing' (e.g. Piaget, 1974; Karmiloff-Smith, 1995; Spelke, 2000). Their exploration is goal-directed and sensitive to a range of object characteristics (e.g. Ruff et al., 1992; Oakes et al., 2012). Children seem to interact systematically with their surroundings, seeking explanations 'like a scientist', testing and refuting various hypotheses (Gopnik, 2000; Legare, 2012). An especially influential view is that children learn by using probabilistic models* like Bayesian networks* , where causal structure is represented through a series of interconnected, random 'nodes' (the causal events), where each connection ('edges'; the causal relations) has an associated value (Glymour, 2003; Gopnik and Schulz, 2004; Tenenbaum et al., 2006). However, these abilities are believed to be unique to humans (Povinelli and Dunphy-Lelii, 2001; Buchsbaum et al., 2012).

Lastly, the interdisciplinary structural-mechanistic model (e.g. Tolman and Krechevsky, 1933; Gibson, 1988; Renner, 1990; Bajcsy, 1989; Chemero and Heyser, 2005; Lopes and Oudeyer, 2010), considers sensory information and how the environment provides and constrains it. The model considers what action possibilities the environment and its objects provide for the animal ('affordances'*), bearing in mind the individual's abilities and specific sensorimotor apparatus (Gibson, 1962; Chemero, 2003; Turvey and Carello, 2011). Many projects in artificial intelligence have taken this approach: to design cognitively flexible robots, explicit, formalised models are needed to overcome the constraints imposed on the robot. These allow it to maximise the information gained and take active control of its environment (Sussman, 1973;

Bajcsy, 1989; Hawes et al., 2010; Lopes and Oudeyer, 2010). The robots should be programmed to detect their errors and deal with them appropriately. The majority of cognitive robots utilise probabilistic learning mechanisms, but few can yet cope with realistic environments beyond specific tasks. This 'designer-based approach'* emphasises the importance of investigating the structure of animal exploration (Krechevsky, 1932; Chappell and Sloman, 2007). In particular, the rat (*Rattus norvegicus*) and the octopus (*Octopus vulgaris*) are two exploratory animals, living in very different environments and possessing different sensorimotor anatomies, which have been studied using structural-mechanistic models (e.g. Renner and Seltzer, 1994; Grasso and Basil, 2009).

This thesis takes elements from all four of the above models, and combines them into a coherent, singular approach to examining exploration. Not only will the underlying cognitive-behavioural strategies be considered, but also the sensorimotor foundations of those behaviours and the effect of the environment upon them. Note this is only in reference to the exploration of the individual. Therefore, this thesis does not consider any social factors involved in learning, although they also play an important role (for a review and some examples see Huber et al., 2001; Heyes, 2011).

The focal animal is the parrot (order Psittaciformes, with cockatoos, collectively known as psittacines*; Birdslife International, 2011): this is an ideal organism for investigating exploration, being naturally exploratory throughout their lives, as well as possessing impressive cognitive capacities, and an anatomy adapted for dexterity (Luescher, 2006). A comparative study with human children was also conducted, as we humans face many of the same

general problems as parrots by living in an ever-changing environment. Like parrots, we have adapted by developing flexible cognitive capacities, manipulatory dexterity and a highly exploratory nature (Buchsbaum et al., 2012).

Part I focusses on the sensorimotor adaptations for exploration; beginning with the the cross-modal interaction between psittacine visual fields and the tactile bill tip organ in chapter 2, before progressing onto the core motor aspects of exploration. This is divided into two broad phases: the approach to an object (chapter 3) and the manipulation of an object (chapter 4).

Conversely, Part II takes a top-down approach to exploration, considering its long-term environmental influences. Parrots were housed in enriched and unenriched environments and their behavioural diversity measured within their home cages and under behavioural test conditions (chapter 5).

Lastly, Part III considers the various cognitive mechanisms and behavioural strategies that may underlie exploration. In chapter 6 and chapter 7, a series of comparative experiments were conducted on parrots and human children respectively.

The sensorimotor and cognitive adaptations found are discussed in chapter 8 within a computational, information-processing context. Implications for other animals' exploratory learning are contemplated, highlighting the fact that there are still many fruitful research directions to pursue.

Part I

Sensorimotor Foundations of Exploration

CHAPTER 2

The interaction of vision and touch during exploration

Material from this chapter has formed part of a publication (Demery et al., 2011).

Parrots are exceptional among birds for their high levels of exploratory behaviour and manipulatory abilities. It has been argued that foraging method is the prime determinant of a bird's visual field configuration. However, here we argue that the topography of visual fields in parrots is related to their playful dexterity, unique anatomy and particularly the haptic information that is gained through their bill tip organ during object manipulation. We measured the visual fields of Senegal parrots using the ophthalmoscopic reflex technique and also report some preliminary observations on the bill tip organ in this species. We found that the visual fields of Senegal parrots are unlike those described hitherto in any other bird species, with both a relatively broad frontal binocular field and a near comprehensive field of view around the head. The behavioural implications are discussed and we consider how extractive foraging and object exploration, mediated in part by haptic cues from the bill, has led to the absence of visual coverage of the region below the bill in favour of more comprehensive visual coverage above the head.

2.1 Introduction

FOR many animals, vision is the main sense used for gaining information about the position and physical properties of objects in the surrounding environment (Hughes, 1977). In conjunction with head and body movements, the visual field* of an animal governs what can influence an animal's behaviour from moment to moment (Ficken, 1977; Fagen, 1985; Power, 2000). Among birds, parrots and cockatoos are exceptional for their high levels of exploratory behaviour and manipulatory abilities (Collar, 1997; Rowley, 1997). These are made possible by distinctive morphological adaptations of the bill, feet and tongue (Whittow and Sturkie, 1999), and highly developed cognitive abilities (Gibson, 1988; Jarvis et al., 2005; Huber and Gajdon, 2006). We ask whether these are complemented by sensory adaptations, principally vision and haptic* (i.e. tactile) cues perceived by the bill tip organ* (Goujon, 1869). Additionally, we ask whether parrot visual fields differ from those of other birds.

It has been proposed that avian visual field configuration is primarily determined by foraging technique (Martin, 2007, 2009). Birds that peck or lunge for their food (e.g. starlings, Sturnidae; or herons, Ardeidae; Martin, 1986a; Martin and Katzir, 1994), or take prey in their feet (e.g. eagles, Accipitridae; Martin and Katzir, 1999) require accurate visual control of the bill or foot position. This has evolutionarily favoured relatively narrow (20^o – 30^o) but vertically long (120^o – 180^o) binocular fields* centred about the bill. However, this results in large blind areas to the rear, requiring increased vigilance behaviour against predators (Guillemain et al., 2002). This is overcome in birds that do not need accurate visual guidance of bill position, such as tactile probers* (e.g. woodcocks, *Scolopax rusticola*; Martin, 1994) and filter feeders*

(e.g. mallards, *Anas platyrhyncho*; Martin, 1986b). Here, the bill falls at the periphery of the frontal binocular field, which is very narrow (approximately 10°) and stretches above the head, providing comprehensive coverage of the celestial hemisphere*.

Little is known, however, about the visual fields of extractive foraging* birds. Psittacines display dextrous manipulatory abilities not only in extracting embedded food items, but also in exploring non-food items. Such manipulation is achieved by coordination of zygodactyl* feet (allowing a secure grasp of objects), and a highly curved maxilla* and a muscular tongue (Homberger, 1980, 2003; Zweers and Berkhoudt, 1994; Collar, 1997; Rowley, 1997). Furthermore, the maxilla is joined to the skull by a synovial joint* (in all other birds the maxilla is fused to the skull), enabling independent movement of both upper and lower jaws (Whittow and Sturkie, 1999; King and McLelland, 1979; Tokita et al., 2007; Tokita, 2004). Object manipulation in psittacines is supported by a comparatively large mesopallium* and a highly investigative nature (Gibson, 1988; Jarvis et al., 2005; Huber and Gajdon, 2006; Lefebvre et al., 2004; Iwaniuk et al., 2005). While in most birds neophilia* is restricted to juvenescence*, in psittacines it continues throughout life, even in situations not directly motivated by food (Luescher, 2006). This suggests that exploration and object play are important for continually updating information within a dynamic environment (summarised in Power, 2000). Therefore, we investigated whether parrot visual fields have an additional function to the traditional drivers of avian visual field configuration: foraging and predator detection (Martin, 2007, 2009).

Psittacine eyes are positioned laterally and high in the skull, suggest-

ing their visual fields are unlikely to resemble those of visually guided foragers. Availability of somatosensory* information from the bill tip organ (Goujon, 1869; Necker, 1972; Gottschaldt and Lausmann, 1974; Berkhoudt, 1979; Gentle and Breward, 1986; Cunningham et al., 2007, 2010) during object manipulation may have allowed the visual field to extend above the head, providing extensive coverage of the celestial hemisphere. The somatosensory area of the brains of parrots predominantly represents the bill and tongue, followed by the feet (Stingelin, 1965; Wild, 1981; Wild et al., 1997; Sultan, 2005; Gutierrez-Ibanez et al., 2009). The psittacine bill tip organ probably consists of groups of mechanoreceptors* embedded in pits at the tip and along the inner ventral edges of the hard keratin* (rhamphotheca*) of the bill, as well as in the tongue (Goujon, 1869). By contrast, the bill tip organs of tactile guided foragers (e.g. ducks and geese, Anatidae; or shorebirds, Scolopacidae) are embedded in the bone of the maxilla and mandible beneath the keratin (Gottschaldt and Lausmann, 1974; Berkhoudt, 1979; Piersma et al., 1998). Psittacine bill tip organs, it seems, have not been studied since the initial descriptions by Goujon (1869), so here we provide further description and consider how haptic information may complement visual information during object manipulation and extractive foraging.

Our chosen study species was the Senegal parrot (*Poicephalus senegalus*), which we believe is a typical representative species of the Psittaciformes. Senegal parrots are resident across West Africa, inhabiting woodland and savannah. Their diet, like the majority of other psittacines, consists of seeds, nuts, blossoms and fruit (Alderton, 2005; Athan and Deter, 2009). Senegal parrots also show the characteristic psittacine exploratory tendency, which lasts throughout their long life (approximately 30 years; Collar, 1997). Their

hook-like maxilla is used both for climbing and object manipulation (Z. P. Demery, J. Chappell and G. R. Martin 2011, personal observations). They use the same method of extracting seeds as found in nearly all Psittaciformes (Collar, 1997). This is where, aided by the foot and tongue, a seed is held delicately between the mandibles and the lower mandible crushes the husk. Then the seed is rotated in the bill and the remaining husk is removed.

In summary, we measured the visual fields of Senegal parrots and asked whether the features of these visual fields can be related to extractive foraging and/or the acquisition of information associated with exploration. Additionally, since parrots could also gain haptic information about objects from their bill, we report some preliminary observations of the Senegal parrot bill tip organ.

2.2 Methods

2.2.1 Subjects and housing

Our subjects were two adult captive Senegal parrots (siblings; 5 years old male and female; 15 cm and 12 cm tall respectively). This close relatedness and small sample size is not a problem for visual field measures, because skull morphology (and hence visual field orientation) does not change significantly between individuals, whether related or not (Martin, 2011). This is especially not an issue considering the general measures we are interested in (subsection 2.2.2).

The parrots were housed indoors in a temperature-controlled environment (23 ± 5ºC) on a 12:12 light cycle (dark from 8 pm to 8 am daily). Their

cage size was 2.46 x 2.00 x 2.51 m. They were cleaned out weekly and fed daily at 11 am on a diet of fresh fruit and vegetables and parrot seed mix (Parrot Mix Royale, Copdock Mill, Ipswich, UK). Wood chips (Lillico Biotechnology, Surrey, UK) covered the floor and a range of toys and ropes, as well as water baths were provided for general environmental enrichment.

2.2.2 Visual fields protocol

Visual field parameters (monocular*, binocular and cyclopean* fields) and eye movement amplitudes were measured in the two subjects using the ophthalmoscopic reflex technique. This is non-invasive and well established as the standard procedure for measuring avian visual fields (Martin, 2007; Martin and Shaw, 2010). The procedure involved the restraint of the birds for 20–30 minutes. After the measurements, the parrots were returned to their aviary and monitored for any abnormal behaviour, none of which was exhibited. Following a recent review of the procedure by a UK Home Office Inspector, it was not considered to fall within the regulations that govern licensed procedures with animals. The ethical guidelines of the UK Animals (Scientific Procedures) Act 1986 were followed.

Each subject was securely fastened into a foam cradle with Velcro straps. The head was held at the centre of a visual perimeter (basically the outer rim of a bicycle wheel) by a custom-made holder moulded from hardened Fimo (Eberhard Faber GmbH), mounted on an adjustable steel brace to allow for the unique shape and manoeuvrability of the parrot bill. The back of the head was supported by a Fimo brace. The eye-to-bill tip angle projected at 50^{o} below the horizontal, which was the approximate head position adopted by the birds when held in the hand or in a resting perched position.

The perimeter's co-ordinate system follows conventional latitude and longitude with the equator aligned vertically in the median-sagittal plane of the head. The eyes of the alert bird were examined using an ophthalmoscope* (Keller, Specialist), which was fitted with a 35 W tungsten halogen lamp and a zero dioptre lens. The ophthalmoscope was mounted on a perimeter arm and its latitudinal position read to ± 0.5°. Alignment of the bird's head in the perimeter was such that the ophthalmoscope viewing aperture was essentially moved over the surface of a sphere (radius 320 mm) centred on the mid-point of the line joining the centres of the pupils; the cyclopean projection centre*.

In each eye, the limits of the retinal visual field* were determined as a function of elevation in the median-sagittal plane at 10° ± 1.0° intervals. Specifically, at each angle of elevation α, the ophthalmoscope was moved along the arm and the angle β at which the retinal reflection disappeared from the ophthalmoscope view of the temporal margin of each eye was recorded. Five measurements were made in quick succession at each point where either the retinal reflection disappeared from view, or the ora serrata was judged to be at the centre of the pupil. Each group of judgements was found to be highly consistent with never more than 2° difference in the recorded values at each elevation.

Spontaneous, non-conjugate eye movements were readily observed. The eyes were induced to take up forward (eyes converged towards the front), or backward (eyes diverged) positions by lightly moving a bunch of keys directly in front and behind the bird's head respectively. The procedure was repeated until there appeared to be no change in the extreme positions at which

the ora serrata could be seen over several trials. The difference between the extreme positions at each elevation defined the amplitude of eye movements at each elevation.

The projections of the edges of the pecten* were also recorded. These provide significant landmarks within the visual fields. The pecten is a highly pigmented structure within the anterior chamber of each eye, which provides nutrition to the retina and is situated above the exit of the optic nerve. It is highly vascularised and does not contain any photoreceptors, producing a blind area in each eye. For these measurements, eye movements were not induced and it was assumed that the eyes adopted a mean resting position. At each elevation, the co-ordinates at which the edges of the pecten appeared were recorded three times and the mean determined.

The direction of the optic axis* of each eye was determined by recording the positions at which the first and second Purkinje images* (reflections from the cornea and the lens anterior surface) of the lamp's filament viewed through the ophthalmoscope. Where these images were judged to be superimposed, the perimeter co-ordinates were recorded. Since the perimeter arm had to be varied simultaneously in co-ordinates' directions in order to achieve coincidence of these images, ten separate determinations of the optic axis were observed in each eye. However, perimeter values were found to vary by no more than 2° in either latitude or longitude.

A topographical map of the visual field and its principal features was constructed based on the retinal margin projections as a function of elevation, but two corrections were first applied to the raw data (Martin, 1984). Firstly,

between the trials of the same bird, the results were corrected so that the head angle was the same. Secondly, from the optic axis and the distance between the eyes (as calculated from photographs taken directly above the bird) the data was corrected for viewing from a hypothetical point of view placed at infinity. The correction factor, χ°, was determined by the equation:

$$\tan(x) = \frac{a \sin \beta}{b - \cos \beta} \tag{2.2.1}$$

...where a is half the separation of the nodal points (estimated to equal 22 mm) and b is the perimeter radius. The axes of rotation of the ophthalmoscope are the projection co-ordinates (α, β) of the visual fields. It should be noted that the correction factor χ°, must be added to or subtracted from the β co-ordinate values, depending upon which quadrant of the hypothetical sphere of measurement value of β lies. The values of α and β could be read to an accuracy of $\pm$ 0.25°.

2.2.3 Bill tip organ protocol

If a bill tip organ is present, tactile pits (in which mechanoreceptors are likely to be embedded in bone or in keratin) can be observed with the naked eye (Goujon, 1869; Necker, 1972; Gottschaldt and Lausmann, 1974; Berkhoudt, 1979; Gentle and Breward, 1986; Cunningham et al., 2007, 2010). Four skulls of Senegal parrots held in the collections of the Natural History Museum (Tring, UK) were inspected with the naked eye and photographed, two with and two without intact keratin. The bill tip organs of the two live Senegal parrots were also photographed.

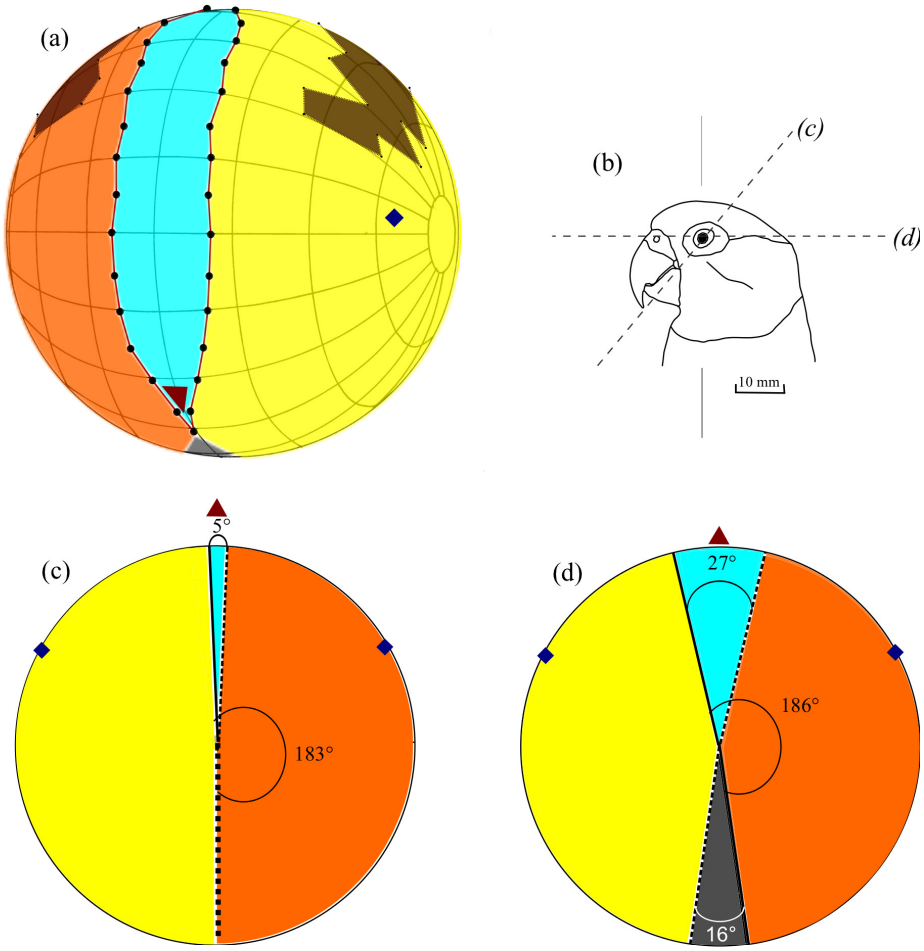


Figure 2.3.1 – Visual fields of Senegal parrots (*Poicephalus senegalus*). **(a)** Perspective view of an orthographic projection of the frontal retinal field (grid at 20º intervals). It shows the region of binocular overlap (blue) between the monocular portion of the left eye (yellow) and right eye (orange) visual fields, as well as the projection of the pectens (brown). The blind area is in dark grey and shows as just a small segment below the bill. The projections of the optic axes are indicated by the diamond points. The bird's head may be imagined to be at the centre of the sphere with its bill tip projecting towards the triangular point in the same posture as depicted in **(b)**. This is the typical resting posture, in which measurements were also taken. Lines *(c)* and *(d)* through the eye refer to the respective diagrams of (c) and (d). **(c)** The section through the visual field in the plane (50º below the horizontal) that passes through the eye and the bill tip (bill tip direction is indicated by a red triangle). In this plane, the binocular field (blue) has a width of only 5º. **(d)** The section through the visual field in the horizontal plane. This is the region where the binocular field has its maximum width (27º). In this plane, there is a blind area behind the head (grey) of 16º. The yellow and orange sectors show the monocular portions of the visual fields of each eye and the full widths of the monocular fields of each eye in these two planes are indicated.

2.3 Results

2.3.1 Visual fields

Four complete sets of visual field measurements (within 2º of each other at each elevation) were made in the male Senegal parrot. Three sets of measurements were made in the female, but, due to practical considerations, we were not able to complete a comprehensive series of measurements at all elevations for this bird. However, in both birds, we recorded unobstructed measurements at elevations from directly behind the head through an arc to below the bill tip. When the birds were mounted in the apparatus, the bill holder prevented observation of the visual field boundaries below the bill tip. Nonetheless, when the birds were held in the hand we were able to verify from casual observations that binocularity ended at or just below the bill tip.

Therefore, we combined data from the two birds to describe a mean visual field; a common technique found in several other avian visual fields studies (Martin, 2011). Figure 2.3.1 shows a map of the mean frontal visual field, as well as horizontal sections through the visual field in the horizontal plane, and in the plane of the eye–bill tip projection (50º below the horizontal). The width of the binocular field as a function of elevation in the median–sagittal plane in the male bird is shown in Figure 2.3.2.

Binocular field

The region where binocularity occurs is vertically long (190º) and narrow, and extends from just below the bill tip to behind the head about 40º from the vertical plane (Figure 2.3.2). The maximum width is 27º and occurs at the

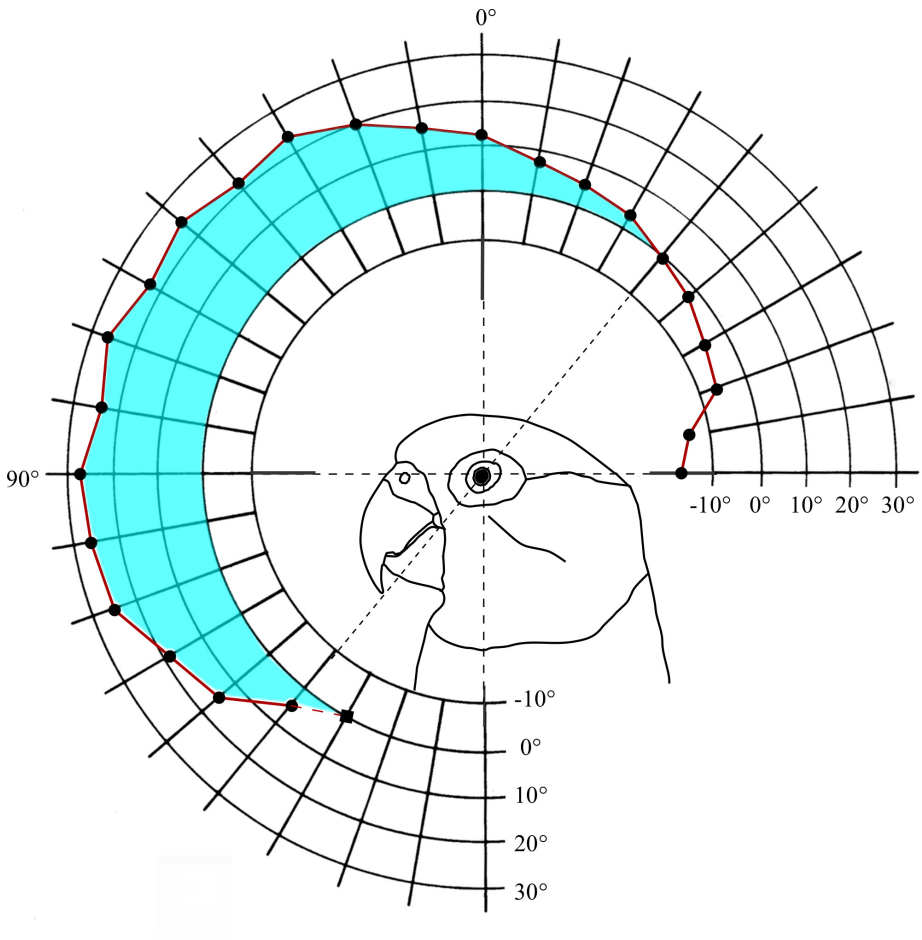


Figure 2.3.2 – Binocular field width in Senegal parrots (*P. senegalus*) as a function of elevation in the median-sagittal plane. The orientation of the bird's head is shown diagrammatically. The last point at 150° elevation has been extrapolated. Note that where the binocular field (shaded in blue) ends, the blind areas below and behind the head begin.

horizontal plane. The binocular area covers approximately 8% of the total horizontal width of the visual field, or 6% of the total visual field sphere. It is of a similar width (approximately 20°) throughout most of its vertical extent. Where the bill tip projects, the binocular width is only 5° and there is a blind area directly below the bill.

Monocular fields

Each eye has a monocular retinal field of 186° in the horizontal plane (Figure 2.3.1d) and approximately 88% of the total visual field in the horizontal plane has monocular visual coverage. This is true nearly throughout the vertical extent of the visual fields, as illustrated in Figure 2.3.1c in the plane of the bill tip projection, where each monocular field is 183°.

Cyclopean fields and blind areas

The cyclopean field covers approximately 98% of the celestial hemisphere; 344° in horizontal plane (Figure 2.3.1). A blind sector begins approximately 50° beyond the vertical plane to the back of the head, and widens to 16° at the horizontal. The pecten in each eye projects from 40° above the horizontal to 10° beyond the vertical plane. The parrot is technically blind in these areas, which cover approximately 10% of the celestial hemisphere, but they can be abolished effectively by the large amplitude of eye movement.

Eye movements

Maximum eye movement amplitude is 24° and eye movements of about this amplitude were found through a range of 60° of elevation in the region of the binocular frontal field. Owing to the small degree of maximum binocular overlap, these eye movements mean parrots can abolish binocularity. Eye movements are non-conjugate and can, therefore, produce asymmetrical visual fields.

Optic axes

The eyes project laterally, with the optic axes oriented slightly above the horizontal plane (13°), and 28° forward. The optic axis of an eye is likely to be

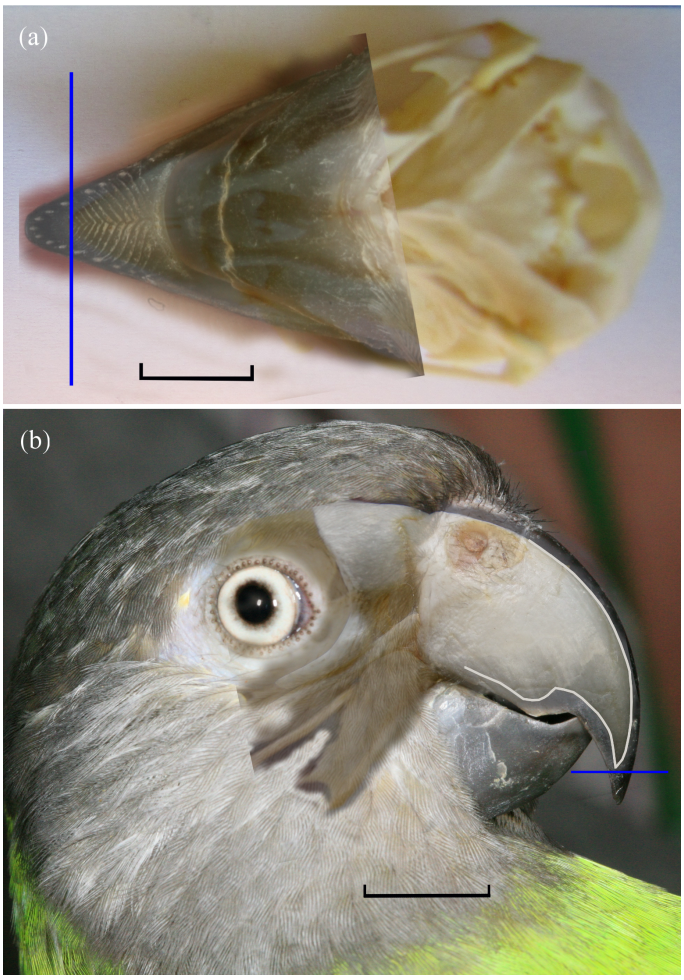


Figure 2.3.3 – Location of the bill tip organ in a Senegal parrot (*P. senegalus*). The scale bars are each equal to 10 mm. **(a)** A ventral view and **(b)** lateral view of a Senegal parrot skull superimposed on a photograph of a live bird to illustrate how the keratin, in which the bill tip organ is embedded, extends the bill into a hook-like structure beyond the maxilla bone. The blue line in both diagrams indicates approximately where the bone ends.

the direction of highest optical quality within a visual field and is therefore also likely to coincide with the direction of highest visual acuity* in each eye.

2.3.2 Bill tip organ

Figure 2.3.3 shows photographs of the Senegal parrot maxilla. Seven pairs of pits within the rhamphotheca can be seen along the edges, with a single

pit at the bill tip. These pits probably contain clusters of mechanoreceptors (Goujon, 1869; Necker, 1972; Gottschaldt and Lausmann, 1974; Berkhoudt, 1979; Gentle and Breward, 1986; Cunningham et al., 2007, 2010). No trace of structures associated with the bill tip organ was found in the bones (maxilla and mandible) of any specimens that we inspected. We observed irregular grooves leading down towards the bill tip, which may reveal the course of the blood vessels and/or nerve fibres that supply mechanoreceptors embedded in the keratin sheath.

Figure 2.3.3 indicates the hard keratin sheath grows to extend beyond the bone. Also clearly visible are periodic grooves within the keratin, lying distal to the smooth mouth palate, which Collar (1997) suggests aids grip. The junction between these grooved and smoothed sections of keratin lies approximately where the mandible meets the maxilla when the bill is closed. A similar arrangement of tactile pits in the maxilla is found in the mandible but in smaller numbers. This is contrary to Goujon's (1869) descriptions, who found the mandible has a significantly larger number of tactile pits than the maxilla.

2.4 Discussion

We have shown that Senegal parrots have a visual field topography unlike those described hitherto in any other birds. Here, we discuss these differences and whether there are features of the visual fields that can be related to extractive foraging and/or the acquisition of information associated with exploration.

2.4.1 General topography of the psittacine visual field

In birds, two main arrangements of visual fields have been described: those associated with visually guided foraging for food taken directly in the bill or feet and those associated with tactile probing or filter feeding (Martin, 2007). In both types, the binocular field is relatively longer (up to approximately 180°) than it is broad, but its location with respect to bill position differs. Visually guided foragers have a broad frontal binocular field (20° – 30°), within which the bill is centrally placed and there is a blind area above and behind the head. By contrast, in tactile and filter feeders, the bill is at the periphery of the binocular field and there is comprehensive coverage of the celestial hemisphere. Additionally, the binocular field width in filter feeders and tactile probers is narrower (approximately 10°) than in visually guided foragers.

In Senegal parrots a different arrangement is found, which can be viewed as a compromise between the two main visual field types (Figure 2.4.1). The binocular field is relatively broad (approximately 27°), but there is nearly comprehensive coverage of the celestial hemisphere. As in tactile probers and filter feeders, the bill tip projects at the periphery of the visual field (so parrots can just see below their bill tip), but because it projects at a steep angle from the horizontal, absolute coverage of the celestial hemisphere is not achieved. However, by pitching the head back only 40°–50°, parrots could achieve comprehensive visual coverage, enabling them to see predators around the entire horizon.

As another consequence of where the bill tip projects, if Senegal parrots wish to inspect visually objects that lie below the bill, they must either pitch

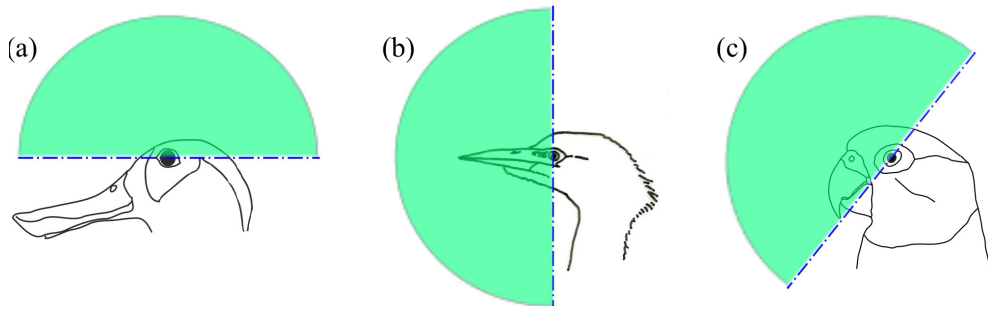


Figure 2.4.1 – The vertical extent of the plane encompassing the ends of the 180° long binocular field (semi-circles shaded in green) in: **(a)** a filter feeding duck (pink-eared duck, *Malacorhynchus membranaceus*); **(b)** a stealth foraging heron (cattle egret, *Bubulcus ibis*); and **(c)** a Senegal parrot *(P. senegalus*). Heads are sketched in profile in their typical resting postures. The psittacine visual field appears to be intermediate between the two archetypal visual field types previously investigated, which have in the past been linked to two distinct foraging techniques (visually-guided foraging versus tactile and filter feeding; Martin, 2007). The dotted blue line is the midline through the eye.

their head forwards to view them binocularly, or turn their head to use the lateral, monocular portion of their visual field. This probably prohibits the rapid and accurate control of the bill towards objects, which is achieved by birds that peck or lunge for their food (Martin, 2009). However, like visually guided foragers, Senegal parrots do have a relatively broad frontal binocular field, which could aid inspection of objects held up in the foot. Parrots are often seen bringing their food items or novel objects up into their field of view with their feet (Whittow and Sturkie, 1999; Luescher, 2006). Psittacines exhibit lateralisation* of visual function (e.g. one eye is often used preferentially for certain tasks) and motor function (e.g. 'footedness' in grasping objects; Friedmann and Davis, 1938; Harris, 1989; Snyder and Harris, 1997; Casey, 2005; Rogers, 1989; Magat and Brown, 2009; Brown and Magat, 2011a). Highest acuity in all avian taxa is thought to occur in the lateral (i.e. monocular) field (Martin, 2009).

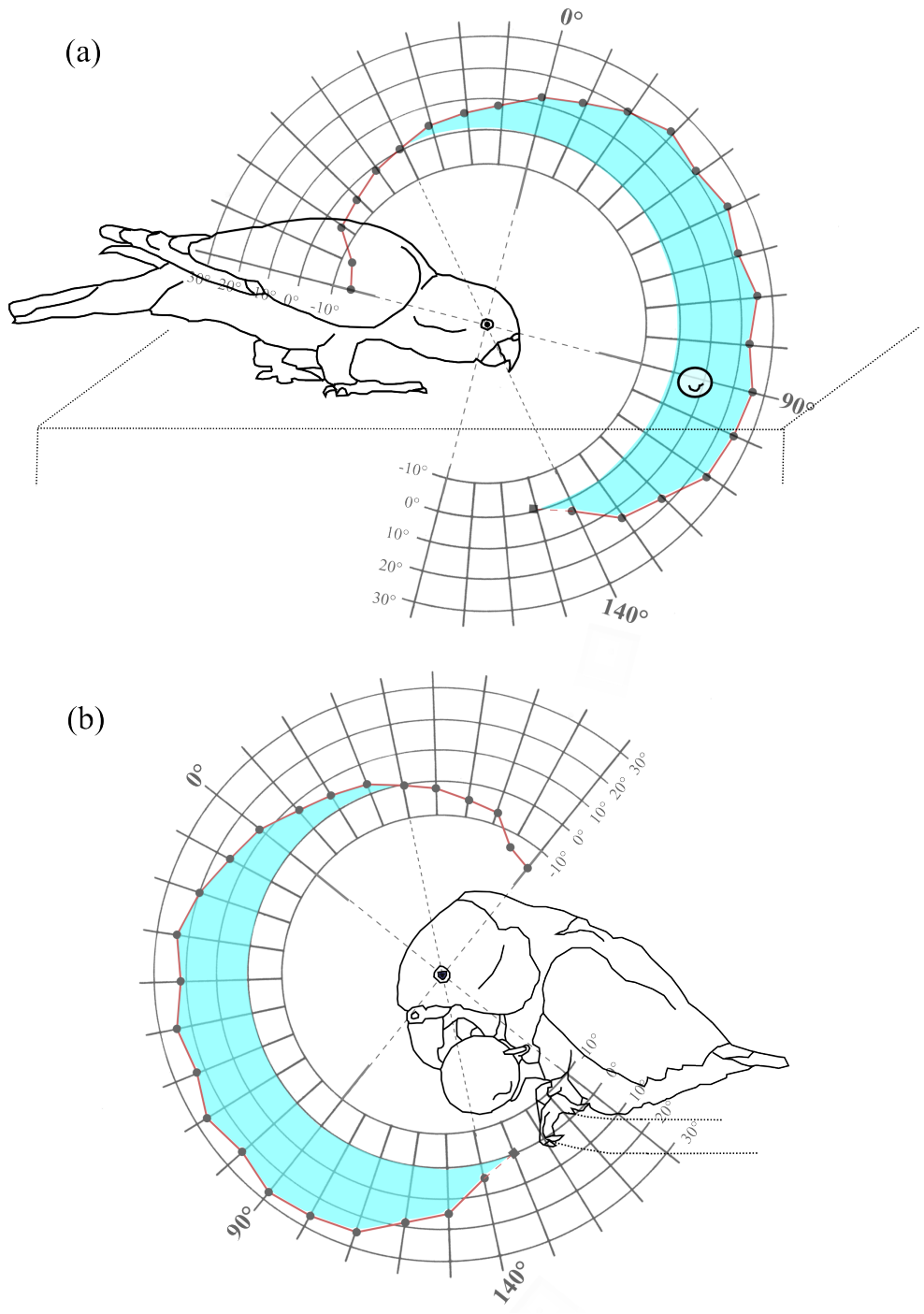


Figure 2.4.2 – Diagrammatic representation of how the psittacine binocular field is orientated during exploration in: **(a)** an approach to an object; and **(b)** manipulation of an object. In both, the binocular field width is plotted as a function of elevation in the median-sagittal plane. Note that where the binocular field (shaded in blue) ends, the blind areas below and behind the head begin. This illustrates that (a) a parrot is likely to approach a target object with its head pitched downwards, so that the object is near the point of maximum binocular width (at 90°), which is thought to be near the point of highest visual acuity. However, once the object is actually grasped (b), haptic exploration*, using the bill tip organ and zygodactyl feet, is likely to dominate visual exploration, as the parrot can only see just below its bill tip. Also the unique shape of the bill obstructs seeing the detail of anything held within the bill.

2.4.2 Extractive foraging and exploration

The tactile pits of the Senegal parrot bill tip organ are arranged along the inside of the curve of the bill tip. This means that unlike other taxa, such as kiwi (Apterygidae; Cunningham et al., 2007; Martin et al., 2007), ibises (Threskiornithidae; Cunningham et al., 2010) and probing shorebirds (Scolopacidae; Piersma et al., 1998), the parrot bill tip organ can only provide information about objects within the bill. Moreover, the unique bill shape obstructs a clear view of an object held within it (Figure 2.4.2b). This suggests items to be explored are typically detected visually first, and the bill tip organ provides haptic information only once an object is grasped.

Thus, parrots can manipulate objects efficiently without further need for visual information. This may have allowed natural selection to favour eyes placed high and laterally within the skull, resulting in extensive visual coverage above and behind the head, presumably for detecting predators and conspecifics. Some birds species that are known to manipulate and position objects carefully between their mandibles, such as hornbills (Bucerotidae; Martin and Coetzee, 2004) and cormorants (Phalacrocoracidae; Martin et al., 2008), have more forward-facing eyes, allowing them to inspect visually items held in the bill. By contrast, parrots seem to have achieved control over objects held in the bill without the need for visual cues.

Both object exploration and extractive foraging are likely to have been important factors in the evolution of psittacine visual fields, as both activities set parrots apart from other birds. However, the visual fields could be seen as facilitating the 'exploratory approach'* towards an object, rather than visual exploration of the object once it has been grasped (during 'ex-

ploratory manipulation'*). Another important factor that may be associated with parrot visual field configuration is the mode of locomotion used during climbing, in which the hooked bill tip is used as a third appendage. When a Senegal parrot climbs, the maximum binocular field width lies forward and above, allowing it to determine the position of the next point it can grasp with its bill. Similarly, it would prove most efficient when walking towards a target object for the parrot to approach with its head pitched downwards and then swung up towards the object just before grasping it with the bill.

What tentative behavioural predictions can be drawn from our description of the Senegal parrot visual field? During exploration, we hypothesise that a parrot would first attend to a novel object or food item using its monocular (left/right) visual field, then on approach pass visual control to the binocular field by orientating its head frontally. The parrot might then continue to tilt its head downwards in the approach towards the object, keeping it within the binocular field, close to the horizontal (as defined in Figure 2.3.1 and Figure 2.3.2). Then the individual may either pick up the object in a foot and bring it to a monocular field (left/right preference; Friedmann and Davis, 1938; Harris, 1989; Snyder and Harris, 1997; Casey, 2005; Rogers, 1989; Magat and Brown, 2009; Brown and Magat, 2011a), or grasp it directly in the bill where haptic exploration* could proceed using the bill tip organ, allowing further understanding of the object's affordances* (Ficken, 1977; Gibson, 1988; Demery et al., 2010; Chappell et al., 2012).

2.4.3 Summary

The Senegal parrot visual field is unlike those described previously in any other bird species. It has both a relatively broad frontal binocular field in the

horizontal plane and a near comprehensive field of view around the head. Although this could be considered a compromise between features described previously in visually guided foragers and the features seen in tactile guided probers and filter feeders, we argue that parrot visual fields are actually associated with their unique anatomy, extractive foraging, exploratory learning and their climbing mode of locomotion. The key to all of these behaviours probably lies in the somatosensory information provided by the bill tip organ, which seems to integrate tightly with information from the Senegal parrots' visual fields. This allows parrots to have foregone visual coverage of the region below the bill in favour of more comprehensive visual coverage above the head, presumably for greater predator and conspecific detection. The ability to manipulate objects with the foot and present them in the monocular visual field for inspection may also have facilitated the evolution of eye position to be high and lateral in the skull.

Thus we have established the possible sensory foundations of exploration in a parrot species, by looking at how the visual field in a Senegal parrot is oriented in relation to its tactile bill tip organ. We will now consider in more detail how the cross-modal interaction* of vision and touch might influence the motor aspects of behaviour (i.e. locomotory/mechanical/grip). We have done this over the next two chapters by broadly dividing the process of exploration into two major phases: the approach to a target object (chapter 3); and the manipulation of a target object (chapter 4).

CHAPTER 3

Visual exploration in approach

Few have considered how animals visually perceive the world while locomoting around it, such as in the exploratory approach towards a novel object. Additionally, virtually no one has looked at bird locomotion beyond flight. Parrots have a distinctive visual field and climbing mode of locomotion, utilising the bill effectively as a third appendage. We varied slope gradient and object height on Senegal parrots' approach towards an object of interest. Then we conducted a video frame-by-frame analysis of this approach, working back from the first bill touch to the object. We discovered that visual perception of a distant object was not hampered by the parrots' climbing when the bill is utilised in climbing. When it was not, parrots kept the object in their visual field near the point of maximum acuity and maximum binocular width. Some preliminary data concerning how parrots employ their monocular versus binocular fields of view as they move closer to an object is also discussed. Whether this unusual mode of climbing or the tactile perception afforded by the psittacine bill tip organ is a greater selection pressure for their visual fields to have evolved above and behind the head remains to be seen.

3.1 Introduction

ANIMALS live in a cluttered environment, yet they can locomote through it, around novel obstacles, and navigate towards a point of interest, seemingly without difficulty (e.g. Fehrer, 1951; Winefield et al., 2002). The

key function of locomotion is to move between two points in space, but as animals move, they can (and need to) gather visual information about the environment around them (Gibson, 1958). This information-gathering (or 'visual exploration⋆') may improve locomotor efficiency itself (e.g. selecting grasp points in climbing or planning routes), but it may also facilitate the collection of information about remote objects of interest (e.g. food items) before they can be grasped (Warren Jr, 1998). Imagine, for instance, a parrot climbing around a forest canopy searching for fruit. A fruit's colour (i.e. ripeness), size and accessibility might all determine whether the parrot chooses that piece of fruit, or if it heads in the direction of another. How the parrot views these different fruit properties is partially governed by its head and body movements, but also by its visual field orientation (Hughes, 1977; Martin, 2007).

We previously measured the visual fields of Senegal parrots (*Poicephalus senegalus*) and found that it is fundamentally different from all other avian visual fields measured to date (Demery et al., 2011, chapter 2). The visual field is shifted above the parrot's hooked bill tip, allowing a comprehensive view of the celestial hemisphere⋆ above the bird's head, but there is also a relatively broad frontal binocular field. It extends 190° from just below the bill tip to behind the head, 40° from the vertical plane. This means the point of maximum binocular width, as well as the point of maximum visual acuity⋆, is at the horizontal plane (along the eye-to-naris⋆ plane).

There are two possible explanations for this shift in the psittacine visual field and its broad binocular field. First, it may be due to the haptic perception below the horizontal plane, provided by touch receptors embedded in

the parrot's bill tip (Goujon, 1869; Demery et al., 2011). Alternatively, it may be due to the distinctive locomotory mode of climbing frequently employed by parrots, whereby they use their hooked bill effectively as a third appendage (Collar, 1997). As a parrot hooks its bill onto a supporting surface, its visual field oriented above the horizontal allows it to still see what is directly ahead, rather than being blocked by the supporting surface (Demery et al., 2011). Unlike primates, who can independently orientate their eyes and their hands during climbing, parrots' eyes are rigidly coupled to one of the appendages they use for climbing (i.e. the bill). This raises questions about whether there is a possible evolutionary trade-off between efficient exploration and efficient locomotion – i.e. between collecting information about distant objects and needing to look where to grasp next.

Parrots are exceptional among birds for their manipulatory abilities and their strong exploratory tendencies, present throughout their lives (Luescher, 2006). They are also thought to be strongly lateralised birds, exhibiting 'footedness'* while manipulating objects (Friedmann and Davis, 1938; Harris, 1989; Snyder and Harris, 1997; Casey, 2005; Rogers, 1989; Magat and Brown, 2009; Brown and Magat, 2011a). This dexterity is further reflected in their locomotion. Utilising their highly curved maxilla, parrots can climb treetops, precarious fruit-bearing branches, vertical surfaces and traverse along the underside of branches (Sparks and Soper, 1990). This mode of locomotion has been described anecdotally by naturalists studying particular species, such as the endangered Puerto Rican amazon (*Amazona vittata*; Warhol and Benirschke, 1986), the thick-billed parrot (*Rhynchopsitta pachyrhyncha*; Bergtold, 1906) and the flightless kakapo (*Strigops habroptila*; Westerskov, 1981). Even species that inhabit open country purportedly spend a significant amount

of time locomoting by this climbing mode (Forsaw, 1977; Hawkins et al., 2001). However, this unusual form of locomotion has attracted little quantitative, systematic work, beyond a brief mention in Zeffer and Norberg (2003). For instance, it is not clear whether parrots predominantly climb by traversing along long branches, or more by climbing between branches, changing direction frequently (an issue highlighted in Bonser, 1999).

Unlike many terrestrial animals, most birds can move through the world by three modes of locomotion: walking, climbing and flight. However, ornithologists have focussed almost exclusively on the biomechanics and anatomy of flight (Norberg, 1979; Heppner and Anderson, 1985; Bonser and Rayner, 1996; Zeffer and Norberg, 2003; Tobalske, 2004; Williams and Bunkley-Williams, 2012). The role of visual fields in walking and climbing, is a previously understudied area for animals, although these locomotory modes have been extensively studied in primates (e.g. Cartmill, 1985; Bonser, 1999; Preuschoft, 2002; Isler, 2003; Thorpe et al., 2007b; Manduell et al., 2011). We nonetheless begin by considering how birds may orientate their heads in relation to their visual fields during flight. This has not yet been studied in psittacines, but has to some extent with pigeons (*Columba livia*; Erichsen et al., 1989; Hodos and Erichsen, 1990; Nalbach et al., 1990; Green et al., 1992). Relatively recently, for instance, Warrick et al. (2002) found that regardless of what environmental conditions they faced, pigeons orientated their heads in isolation from their bodies, in such a way as to allow a clear view of what was in front of them.

We conducted an anecdotal review of 20 photos from ARKive of various parrots in flight (2010; e.g. Figure 3.1.1a–b) and ran a series of preliminary

live observations of two captive Senegal parrots (Z. P. Demery, J. Chappell and G. R. Martin 2011, personal observations). Apart from during take-off and landing, a parrot generally seem to keep its head level in line with its body. This head posture may enable greater aerodynamic efficiency (Witmer et al., 2003; Tobalske, 2007). Alternatively, it may maximise binocularity and visual acuity on the horizontal plane in the intended direction of travel (Hengstenberg, 1988; Green et al., 1992) and to fixate on the remote target object (Goodale, 1983; Erichsen et al., 1989). It is difficult to separate these two explanations.

However, if the latter explanation of maximising binocularity were true, taking into account with what we now know about parrot visual fields, this should hold true for other forms of locomotion, such as walking and climbing. This does indeed seem to be the case from a second ARKive review of 20 photos of parrots traversing branches (e.g. Figure 3.1.1c–e): the area of maximum binocular width and visual acuity generally is oriented in the direction of travel and/or fixated on the remote object of interest. This is, however, very preliminary data and it is difficult to judge angles precisely from others' photographs and videos, as one cannot be sure about the angle of the camera to the subject.

One of the few ornithological studies that has considered avian visual fields in conjunction with a locomotory gait other than flight is that by Cronin et al. (2005). They found that whooping cranes bob their heads as they walk, enabling them to keep a steady visual field for detecting and identifying objects. However, this study was conducted on a level surface, so it did not consider how a slope may affect head orientation during locomotion. This

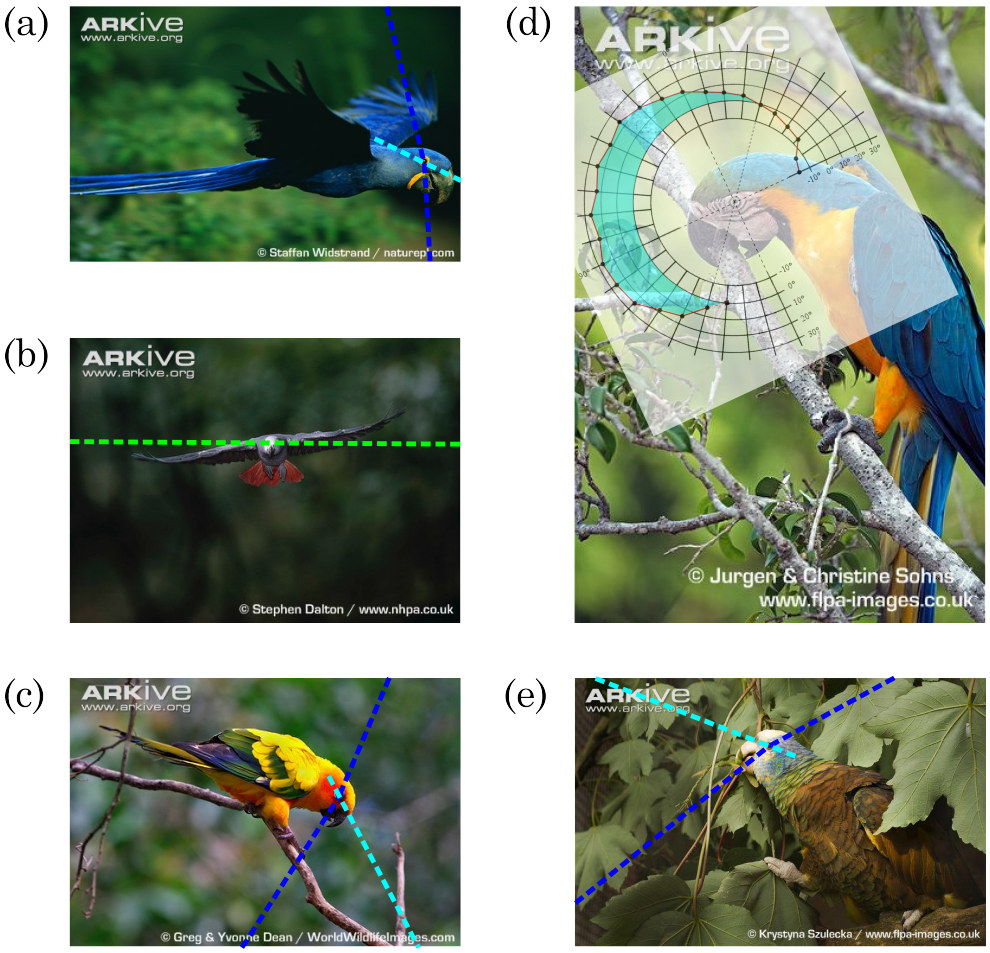


Figure 3.1.1 – ARKive (2010) selection of photographs of various parrot species in flight (a–b) and while climbing (c–e). Note how in each the head is orientated in the direction of travel: in level flight the head is approximately in line with the body, so that the point of maximum binocular width is orientated in the direction of travel; while climbing, this is partially determined by where the bill is on the supporting surface when it is used as a third appendage. The species are as follows: **(a)** Hyacinth macaw (*Anodorhynchus hyacinthinus*); **(b)** African grey parrot (*Psittacus erithacus*); **(c)** Sun parakeet (*Aratinga solstitialis*); **(d)** Blue-and-yellow macaw (*Ara ararauna*; with entire binocular field from Demery et al., 2011); **(e)** St Vincent Amazon (*Amazona guildingii*). The dark blue dotted lines indicates the limits of the binocular field, while the light blue lines indicate the maximum binocular width, and the green line indicates the mid-line through the two eyes.

may be a relevant factor for parrots, when they may transfer from a walking gait into a climbing gait, as the supporting surface becomes steeper.

Green (1998), on the other hand, did consider gradient, but using domestic chicks (*Gallus gallus domesticus*). When they walked up or down a slope, the head angle increased or decreased respectively with the gradient of the slope. He concluded that in many birds head posture control evolved initially as part of general mechanisms using both visual and haptic information to guide vestibular* body posture and the locomotory step cycle. The ensuing retinal image of the environment subsequently constrained the evolution of retinal structure, visual field topography and optical gradients.

However, Green (1998) did not record body posture data in addition to the head posture data to confirm his conclusions. He moreover rejected explanations relating to the optical and physiological properties of the eye (i.e. visual field orientation) largely by drawing comparisons to visual research on pigeons – a very different bird species. Green did not have information about the visual field orientation of the chicks, so he was not able to fully assess how features such as binocularity (e.g. Martin and Young, 1983; Martin, 2009) and/or retinal areas of greater visual acuity (e.g. Ehrlich, 1981; Nalbach et al., 1990; Hodos and Erichsen, 1990), may impact on chick locomotion. Visual fields can vary greatly between bird species, especially considering ecological and locomotory differences (Martin, 2011) – a particularly salient issue when considering the distinctive psittacine climbing gait. Therefore, greater experimental evidence is required. For instance, it is not clear which portion (i.e. binocular or monocular) of the psittacine visual field the object is in on the parrot's approach to it.

Thus, the aim of our study was to examine Senegal parrots' visual field orientation during climbing and walking through two experiments, one for each gait. Following the model set by Green (1998) and Cronin et al. (2005), for simplicity we focussed on birds travelling in a single direction towards a target object, with no obstacles in-between (like a bird traversing along one branch towards a fruit). We considered how the eyes, bill and body were orientated in relation to the object, and to each point of contact on the supporting surface leading to the object. Note that we could not know for certain where in the surrounding environment the parrot was focussing on at any given moment, without more invasive or advanced eye-tracking techniques (e.g. Kjaersgaard et al., 2008; Voss and Bischof, 2009). In the first experiment on climbing, we varied the slope gradient, while in second experiment on walking, we varied the height of the target object from the flat ground. For both experiments, we predict that head orientation will be dependent upon maintaining visual control, while body orientation will be dependent upon maintaining vestibular control. This meant for the first experiment on climbing, we hypothesise:

- head orientation will be determined primarily by the parrot attempting to keep either the target object of interest, or the next point of contact for the bill on the climbing support centred in its visual field (near the point of maximum binocular width and visual acuity);
  - the exception to this will be when the need to utilise the bill becomes greater when climbing steeper inclines, which will in turn affect head orientation;.
- therefore, the head orientation will *not* be dependent on the body orientation (and vice versa);

- instead, body orientation will be dependent on the climbing support gradient to maintain balance.

This independence between head and body orientation should be reflected in the second experiment on walking. However, here the bill is not required for locomotion, so the head is free to orientate solely based on where the object is. Thus, here we hypothesise:

- the head orientation will be determined by the height of the target object, so that the object is again near the point of maximum binocular width;
  - for instance, when the object is at ground level, it will be approached with the head pitched slightly downwards;
- the body orientation will be constant throughout, as the supporting surface gradient does not change.

As parrots have exceptionally large frontal binocular fields for birds, in this walking experiment we also wanted to investigate which portion (i.e. binocular or monocular) of the visual field the object was in on the parrot's approach to it. It is thought that, depending on the type of information required for collection, the monocular fields provide greater resolution than the binocular field, particularly at close range to the target of interest (Martin, 2007). The binocular field is likely more suited for detecting movement, or for processing the optic flow-field* information produced while locomoting (Martin, 2009). Thus lastly we predict:

- the proportion of time the object is in a monocular or the binocular field

will vary with distance from the object, such that;

- the object is first identified in one of the monocular fields;
- then for the main part of the approach, the object is maintained in the binocular field;
- once the parrot is within grasping distance of the object, it is largely maintained in one of the monocular fields again.

3.2 Methods

3.2.1 Subjects and housing

Our subjects were two adult captive Senegal parrots (*Poicephalus senegalus*; siblings; 5 years old male and female; 15 cm and 12 cm tall respectively). They were housed indoors in a temperature-controlled environment (23 ± 5ºC) on a 12:12 light cycle (dark from 8 pm to 8 am daily). Their cage size was 2.46 x 2.00 x 2.51 m. They were cleaned out weekly and fed daily at 11 am on a diet of fresh fruit and vegetables and parrot seed mix (Parrot Mix Royale, Copdock Mill, Ipswich, UK). Wood chips (Lillico Biotechnology, Surrey, UK) covered the floor and a range of toys and ropes, as well as water baths were provided for general environmental enrichment.

Senegal parrots are resident across West Africa, inhabiting woodland and savannah. Their diet, like the majority of other psittacines, consists of seeds, nuts, blossoms and fruit (Alderton, 2005; Athan and Deter, 2009). Senegal parrots also show the characteristic psittacine exploratory tendency, which lasts throughout their long life (approximately 30 years; Collar, 1997). Their hook-like maxilla is used both for climbing and object manipulation (Z. P. Demery, J. Chappell and G. R. Martin 2011, personal observations). They

use the same method of extracting seeds as found in nearly all Psittaciformes (Collar, 1997).

3.2.2 General protocol

We ran two concurrent experiments investigating the climbing and walking approach of Senegal parrots. At a random time during the day, the subjects were presented with both experiments' sets of apparatus in their home cage to minimise neophobia* over five consecutive days for an hour. Mealworms were placed near the entrances of both apparatus sets daily. Additionally, the birds were trained to climb for mealworms around the mesh of their cage in different directions daily for 10 minutes.

The experiments were administered consecutively. Each subject experienced three repeats of each condition in each experiment. Each condition was presented in a random order to each bird, but each repeat of the same condition occurred consecutively. The subject was placed on the bottom rung of the ladder (outside of the tube) in Experiment 1 (subsection 3.2.3), or the start of the tunnel in Experiment 2 (subsection 3.2.4). Then they were left for 1 minute or until they reached the reward at the end. Between trials they were placed on a perch behind a blind, while the apparatus was reset for the next trial. All of the trials were conducted in the presence of both subjects, as they could not be separated. The order of subjects for each trial was randomised.

3.2.3 Experiment 1: climbing approach

Materials

This experiment was recorded by a high resolution video camera placed 1 m away, perpendicular to the apparatus (Sanyo Xacti VPC-CG100; in H264-

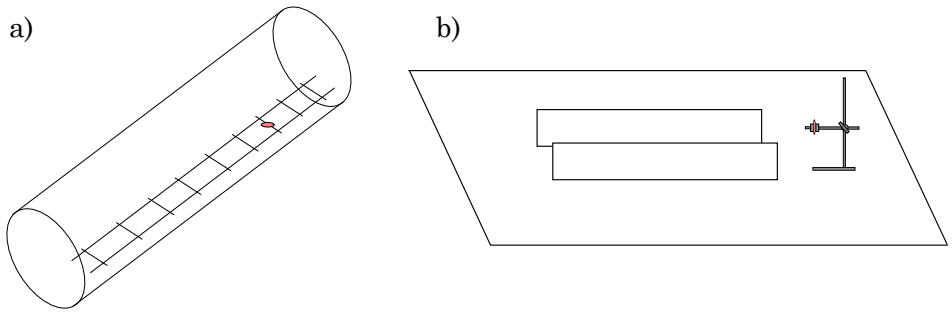
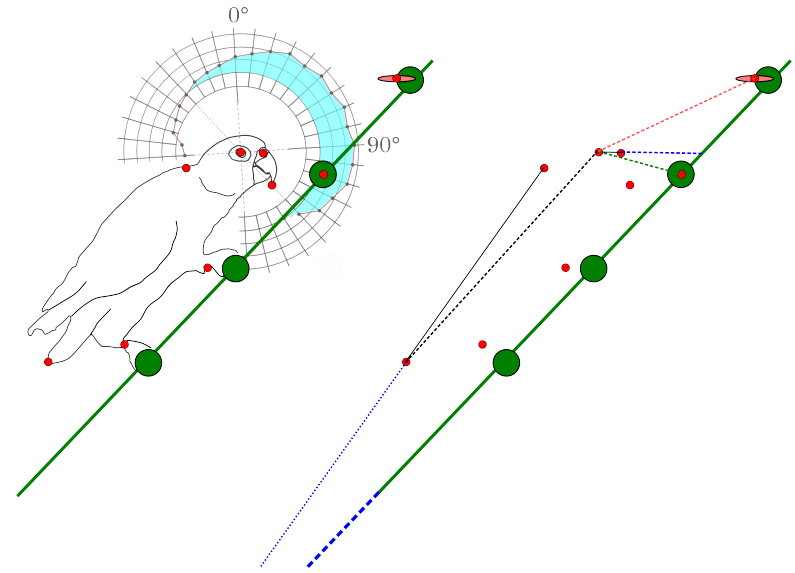


Figure 3.2.1 – A diagram of the apparatus in **(a)** Experiment 1 for measuring the climbing approach of two Senegal parrots (*P. senegalus*), where the parrots climbed up a ladder suspended in a transparent perspex tube; and **(b)** Experiment 2 for measuring their walking approach, where the parrots walked along a transparent perspex 'tunnel'. In both experiments, the target object at the end of the approach was a mealworm: in Experiment 1 it was on the top rung; and in Experiment 2 it was on a G-clamp, whose height could be adjusted.

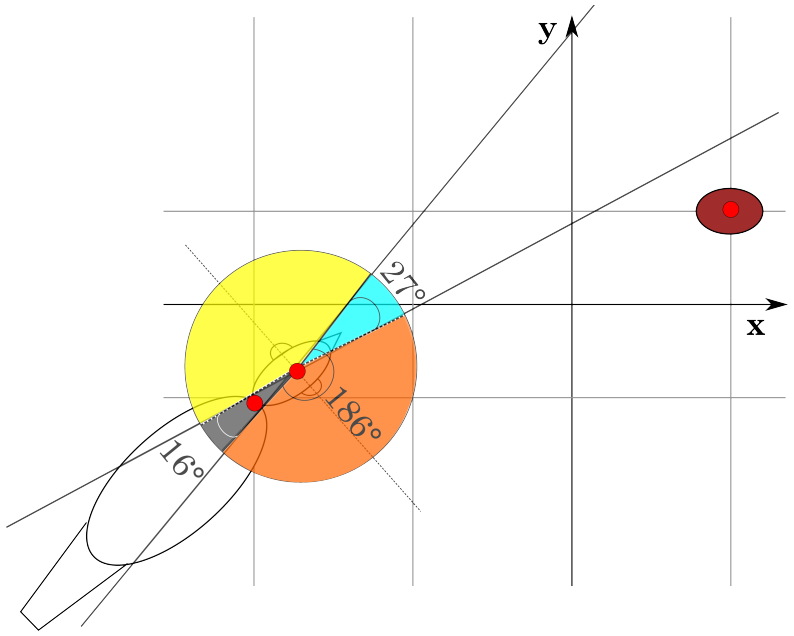
MPEG-4 avc1 codec; 1920x1080 resolution, 60 fps). The supporting surface was a rigid wooden ladder (44 cm long, 8 cm wide) with six different coloured rungs, each about 7 cm apart (Figure 3.2.1a). The middle part of it was fixed in the middle of a transparent perspex tube (20 cm in diameter, 60 cm long), so a Senegal parrot could stand upright on any ladder rung with plenty of space around them, but could only travel in one direction (up/down ladder). A food reward (a mealworm) was fixed to the top rung, 10 cm down from the end of the tube. The reward was clearly visible from the bottom, but it could not be accessed from above. The tube was fixed to the cage mesh. There were four conditions, where the gradient of the supporting surface was either 0° (horizontal), 30°, 60°, or 90° (vertical).

Analytical method

We modelled our analysis method on that of Cronin et al. (2005) and Green (1998). The video files were converted into an image sequence (unscaled JPEG, with interlaced scaling and no compression) using MPEG Streamclip



(a)



(b)

Figure 3.2.2 – A diagram of the analysed points (red dots) on a locomoting parrot from video recordings by: **(a)** a side camera in both Experiments 1 and 2 on the climbing and walking approach; and **(b)** a top camera just in Experiment 2 on the walking approach. The target object at the end of the approach was a mealworm (pink oval in (a) and brown oval in (b)). In (a), the green line is the ladder and the dotted lines show the relevant angles. In (b), the details of the calculations (from the x, y co-ordinates of each point), for which part of the visual field the object is in, are shown in Appendix B. The circle represents a section through the bird's visual field in the plane that passes through the eye and the bill tip (50° below the horizontal). The yellow and oranges areas are the left and right monocular fields respectively. The blue area is the binocular field (as in (a)). The dark grey area is the blind area.

version 1.2 (Cinque, Squared 5srl 2006-08), so a 30-second 60 fps video file would result in approximately 1800 image frames. ImageJ (v. 1.43u 64-bit; Wayne Rasband, National Institute of Health, USA) was used for frame-by-frame analysis every 10 frames per second, working *backwards* from the first point of bill contact with the target object. This meant if each locomotory bout lasted 10 seconds, then in total approximately 3240 frames were analysed. In each frame, the position of the following points were noted: centre of the eye; naris (nostril); maxilla (bill) tip; each intertarsal joint (ankle); mantle (shoulder); and upper tail coverts (tail base; Figure 3.2.2a). From these points, the angle of the body (tail-tip-to-mantle) and angle of head (eye-to-naris) were calculated relative to:

- each other;
- the horizontal;
- the supporting surface;
- the target object (middle of mealworm);
- and the next point of contact.

These points also allowed us to calculate the number of bill touches to the ladder within each condition. Moreover, this data was related to the psittacine visual field using data from Demery et al. (2011). We analysed where the visual field was centred in relation to the experimental apparatus at each point along the bird's gait. The area where the visual field was centred was defined as the point of maximum binocular width (along the eye-to-naris angle, or the 'horizontal plane at 0° elevation' as shown in Demery et al., 2011[1]) ± 20° in the vertical extent of the binocular field. From this,

[1]Note in this chapter 0° is the horizontal and 90° is the vertical, but in chapter 2 90° was the horizontal and 0° is the vertical. The latter was appropriate for visual field elevations, but

we could calculate the percentage of time in each trial the visual field was either centred on the object, next bill contact point or some other area of the apparatus.

3.2.4 Experiment 2: walking approach

Materials

The details of the video recording were the same as in Experiment 1 (subsection 3.2.3), but this experiment was also recorded by a plan-view camera 50 cm above. The apparatus was placed on a small table (1 m by 2 m) in the middle of the home cage (Figure 3.2.1b). A mealworm was held in a G-clamp, whose height could easily be adjusted, at the end of a perspex 'tunnel' (50 cm high, 90 cm long), so it could not be accessed from above. There were 5 conditions, where the target object (mealworm) was either at 0, 5, 10, 15 or 20 cm above the flat surface.

Analytical method

The details of the video analysis were the same as in Experiment 1 (subsection 3.2.3), but the second camera above the apparatus in Experiment 2 allowed estimation of whether the object was in the left monocular, right monocular, or the binocular field at each step. This was then related to distance from the target object. Analysis of distance ended when the object was within grasping distance of the bird (i.e. bird and object 5 cm apart). The following points in the image frames from this video footage were marked (Figure 3.2.2b):

- a consistent point on the back of the head (e.g. white spot in feathering);
- the mid-point between the eyes;

not for slope gradients.

- and the middle of the mealworm.

These points were chosen so that the general position of the object in the visual field at any given moment could be calculated by trigonometry (Appendix B). These trigonometry calculations thus made the following assumptions:

- Take a top-down, two-dimensional view of the bird in relation to the object along the x, y-axes (Figure 3.2.2b), so discount any head movements along the z-axis for instance;
- Assume the bird always orientates its head to focus on the item of interest in the plane/elevation of maximum binocularity (as shown in Demery et al., 2011);
- Assume that the eye is looking in the 'average direction', but there will an error of ± 20^o due to non-conjugate eye movement.

3.2.5 Statistical methods

The effects were analysed using repeated measures General Linear Models. The assumptions of parametric methods (normality of error, homogeneity of variance and linearity) were confirmed from plots of coefficients versus fitted values. All analyses were performed using Minitab® Statistical Software version 15.1.30. The probability level accepted for significance was $p < .05$.

For both experiments, we focussed on analysing three key angles: body-head; body-slope; head-slope. We tested whether slope gradient or object height had an effect on each of these angles. These were analysed for each bird within each trial, taking a mean from the entire trial time (i.e. the entire gait). All of the angles data was offset by 90, then Box-Cox transformed,

where $\lambda = 2$ in Experiment 1 and $\lambda = 4$ in Experiment 2. For each model, the other angles were built in as covariates. Where proportional data measures were used to test the effect of gradient on the location the visual field centred on, the data was arcsine-squareroot transformed. In Experiment 2, we analysed whether the distance between the target object and the bird had an effect on the proportion of time the object was viewed using the monocular field (versus the binocular) using a repeated-measures one-way ANOVA.

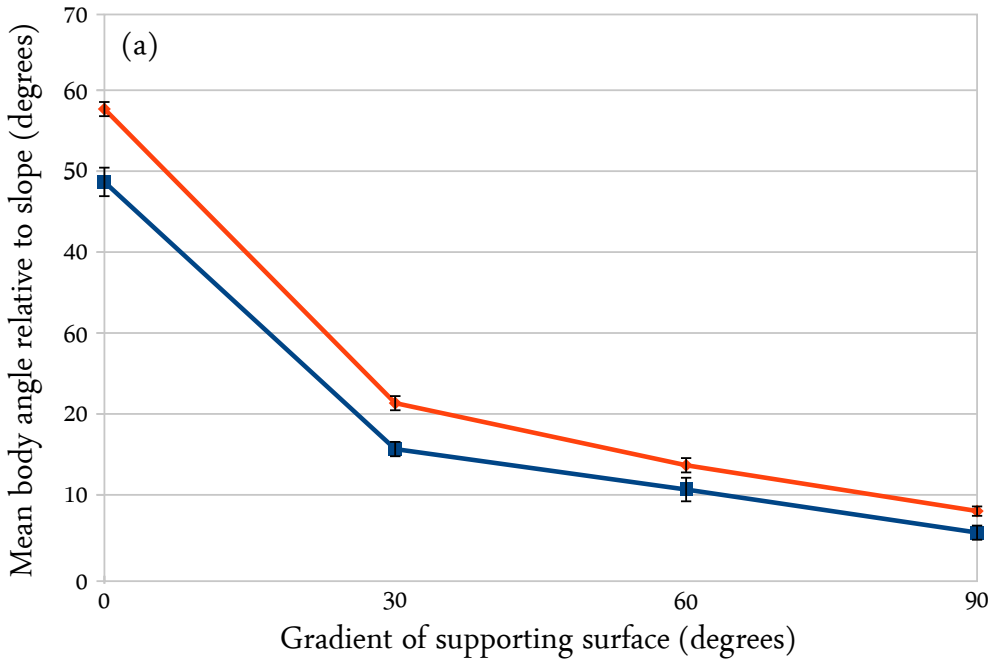
3.3 Results

3.3.1 Experiment 1: climbing approach

Head angle and body angle

While climbing, the supporting surface gradient did not have a significant effect on the Senegal parrots' body angle (mantle-tail angle) relative to the head angle (eye-naris angle; GLM: $F_{3,14} = 1.36$; $p > .05$; Table 3.1). However, the gradient condition did have a significant effect on the body angle relative to the supporting surface (or relative to the horizontal; GLM: $F_{3,14} = 44.16$; $p < .01$). In other words, as the angle of the slope became steeper, so did the angle of the body (Figure 3.3.1a). Within a trial, the body angle remained relatively constant throughout the climb.

The supporting surface gradient did not have a significant effect on the mean head angle within each condition relative to the supporting surface (or the horizontal; GLM: $F_{3,14} = 0.21$; $p > .05$). Within the horizontal gradient condition, the head angle relative to the target object was fixed at $0^o \pm 21^o$ throughout the gait, so that the target object was in the centre of the visual field (section 3.3.1). However, as the gradient of the supporting surface in-



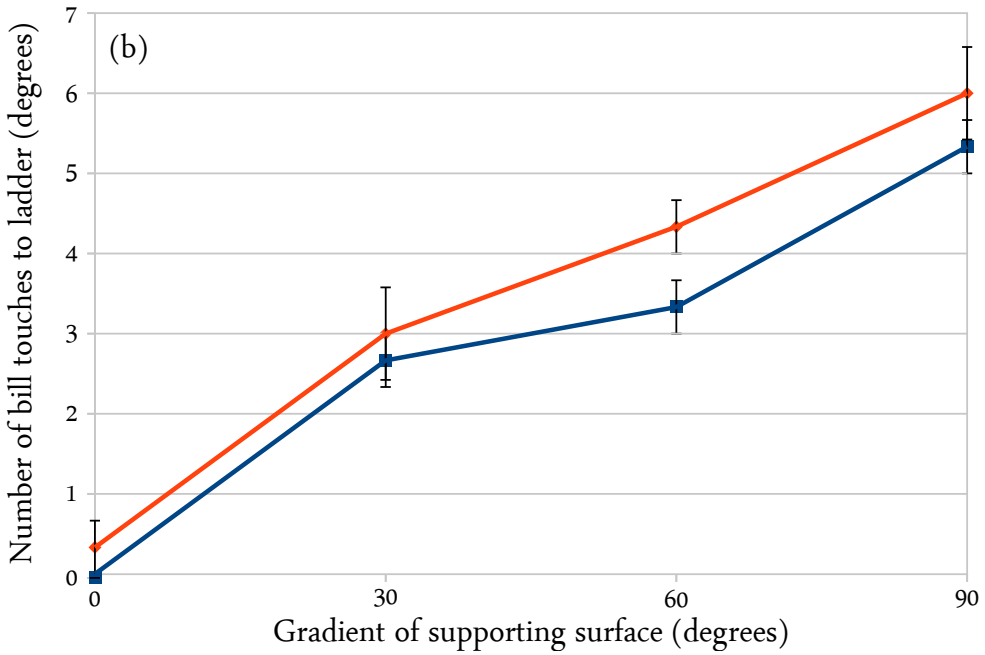


Figure 3.3.1 – Line graphs illustrating what the body angle and the head angle were dependent on while climbing, against the gradient of the supporting surface (varied from 0° to 90° in Experiment 1). **(a)** The body angle in relation to the supporting surface. **(b)** The mean number (out of three repeats) of bill touches to the supporting surface. The red lines are the male Senegal parrot (*P. senegalus*) and the blue lines are the female Senegal parrot. The error bars represent standard-error-of-the-mean, where the mean was each bird's mean across three trials in each condition.

Table 3.1 – A summary table outlining the three repeated measures GLM model for the effect of supporting surface gradient on head-slope angle, body-slope angle and body-head angle respectively in Experiment 1. Gradient was a fixed variable (0, 30, 60 and 90 degrees). For each model, the other angles and the number of bill touches to the supporting surface were included as covariates. All of the angles data was offset by 90, then Box-Cox transformed, where $\lambda = 2$.

	Factor	**d.f.**	***F***	***p***
Head-slope	Gradient	3	0.21	0.886
	Bill touches	1	0.52	0.482
	Body-slope	1	0.01	0.938
	Body-head	**1**	**6.81**	**0.021**
Body-slope	**Gradient**	**3**	**44.16**	**< 0.001**
	Bill touches	1	0.28	0.608
	Head-slope	0.01	0.01	0.938
	Body-head	1	1.26	0.281
Body-head	Gradient	3	1.36	0.297
	Bill touches	1	1.66	0.219
	Head-slope	**1**	**6.81**	**0.021**
	Body-slope	1	1.26	0.281

Significant variables are indicated in bold; $n = 24$ for all measurements.

creased, the number of bill touches to the supporting surface increased (Figure 3.3.1b). In other words, as the bill was employed more as part of the climbing gait as the slope gradient increased, the head angle (relative to the target object and relative to the supporting surface) was no longer constant throughout the gait within a trial.

Position of target object in visual field

For each bird in each condition in Experiment 1, at every point along the ladder, the target object was within the visual field, even when the bill was in contact with the supporting surface. However, with steeper gradients, the birds increasingly employed their bill in climbing (Figure 3.3.1b), so, the

Table 3.2 – A summary table outlining the GLM model for the effect of supporting surface gradient on the proportion of time (dependent variable) the visual field was centred upon each location in Experiment 1. Gradient (0, 30, 60 and 90 degrees) and location (next bill contact point, target object or another point) were fixed variables. The proportional data was arcsine-squareroot transformed.

Factor	**d.f.**	***F***	***p***
Gradient	3	2.08	0.161
Location	**2**	**214.61**	**< .001**
Gradient × Location	**6**	**116.79**	**< .001**

Significant variables are indicated in bold; $n = 24$ for all measurements. Post-hoc Tukey on interaction: all $p < .05$.

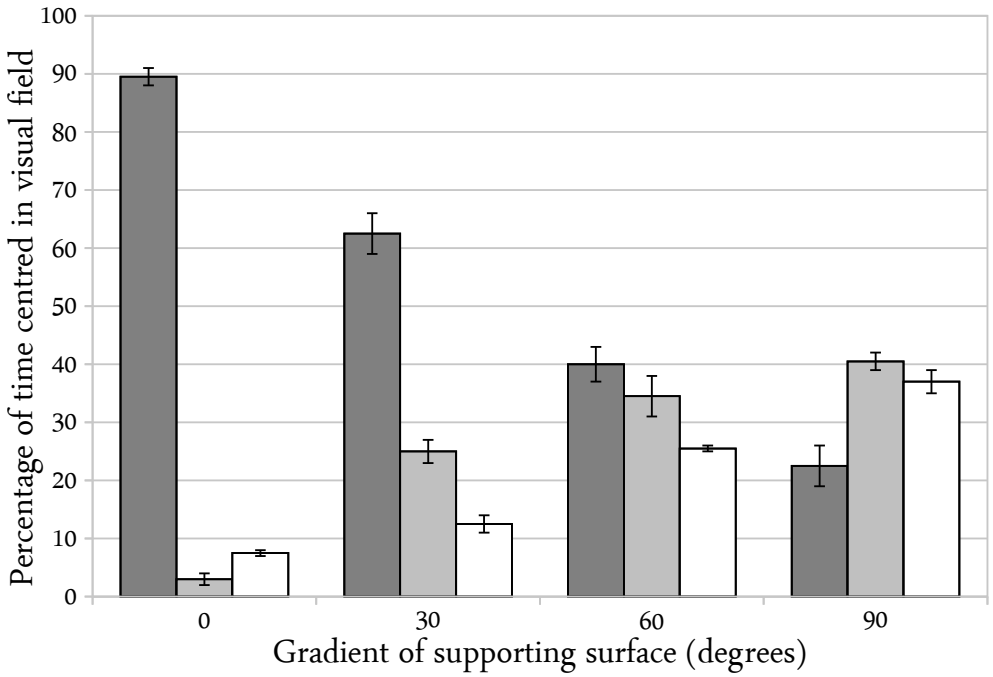


Figure 3.3.2 – A bar chart showing, at each gradient condition in Experiment 1 on climbing, the mean percentage of time within a trial the visual field either centred on: the target object (dark grey); the next point of contact for the bill on the supporting surface (light grey); or somewhere in between (white). The area the visual field was centred on was defined as the point of maximum binocular width ± 20° in the vertical extent of the binocular field (see Figure 3.2.2a). Note that the target object and the next point of contact were still always found to be within the visual field limits, even it it was not always centred upon each. The error bars represent the standard-error-of-the-mean, where the mean was across two birds, experiencing three repeats of each condition.

target object was decreasingly near the centre of the visual field (i.e. the point of maximum binocular width ± 20°), but instead more towards the visual field's periphery. At the most extreme head-object angle, when the bill was hooked onto a ladder rung, the object was at 10° past the vertical (350°), but this was still 30° from the edge of the visual field.

Thus, depending on the bird's location along the ladder, the centre of the visual field was on either the next point of contact for the bill, or the target object. Figure 3.3.2 illustrates the significant interaction between the supporting surface gradient and proportion of time the visual field is centred on upon each location (GLM: gradient*focussed area; $F_{6,11} = 1116.79$; $p < .001$; Table 3.2). As the gradient became steeper, the parrots spent less time focussing on the target object, while the proportion of time the visual field is centred on a surface contact point increased (Tukey: all $p < .05$).

3.3.2 Experiment 2: walking approach

Head angle and body angle

While walking, the height of the target object did not have a significant effect on the Senegal parrots' body angle relative to the supporting surface (GLM: $F_{4,21} = 0.30$; $p > .05$; Table 3.3). Throughout Experiment 2's conditions, the body angle relative to the horizontal supporting surface stayed at a constant angle of approximately 51° (± 12°). The bill was not employed for locomoting throughout this experiment and so did not touch the supporting surface.

The object height condition did have a significant effect on the head angle relative to the supporting surface (GLM: $F_{4,21} = 212.33$; $p < .01$; Figure 3.3.3). When the object was on the ground, both parrots throughout their walking

Table 3.3 – A summary table outlining the two GLM models for the effect of target object height from ground on the body-slope angle and the head-slope angle in Experiment 2. Object height (0, 5, 10, 15 and 20 cm) was a fixed variable. For each model, the other angle was included as a covariate. All of the angles data was offset by 90, then Box-Cox transformed, where $\lambda = 4$.

	Factor	d.f.	*F*	*p*
Body-slope	Object height	4	0.30	0.874
	Head-slope	1	0.00	0.996
Head-slope	**Object height**	**4**	**212.33**	**< .001**
	Body-slope	1	0.00	0.996

Significant variables are indicated in bold; $n = 30$ for all measurements.

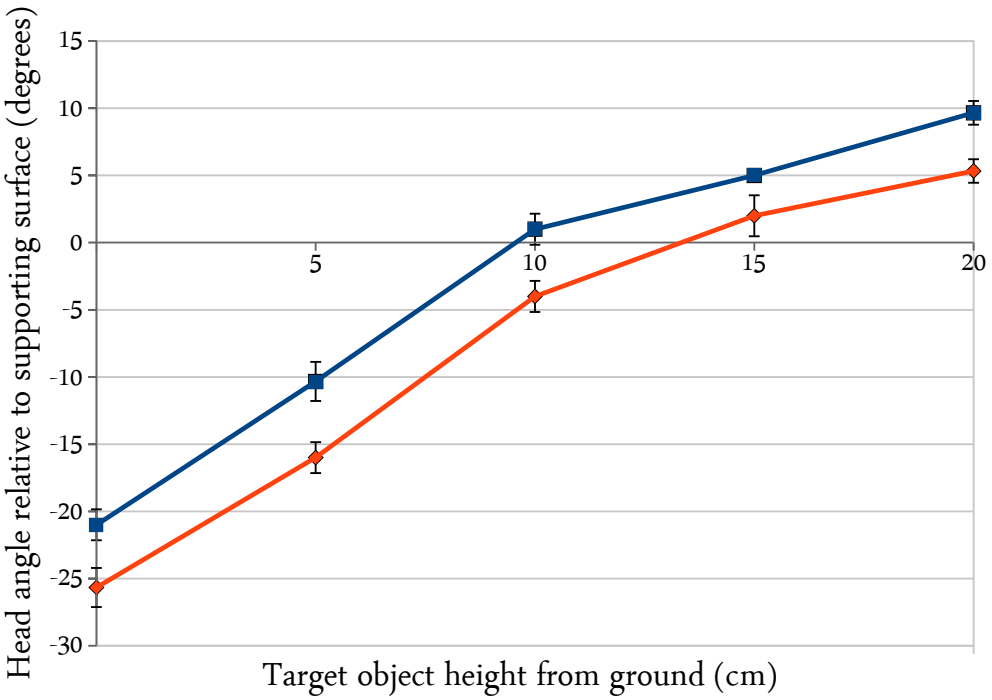


Figure 3.3.3 – A line graph illustrating how the head angle (relative to the supporting surface) changes as the height the target object is at from the ground was varied in five conditions in Experiment 2 on walking approach. The red lines are the male Senegal parrot (*P. senegalus*; height 15 cm) and the blue lines are the female Senegal parrot (height 12 cm). The error bars represent standard-error-of-the-mean, where the mean was each bird's mean across three trials in each condition.

approach held their head at a constant angle relative to the supporting surface, at 25º ± 9º below the horizontal (i.e. -25º in Figure 3.3.3). Here the target object was in the visual field near the point of maximum binocular width (as in first condition of Experiment 1; subsection 3.3.1). However, as the height of the target object from the ground increased, the angle of the head relative to the supporting surface significantly increased (Tukey: all $p < .01$).

Position of target object in visual field

A mean calculated across all trials and both birds showed that the binocular field was used to view the target object for an approximately equal proportion of the trial time as the monocular field. When the monocular field was utilised, both birds used the right monocular field for approximately 78% (± 3%) of the trial time, rather than the left monocular field.

There was a significant effect of distance of the parrot from the target object on the proportion of time the object was in the monocular field (repeated one-way ANOVA: $F_{7,8} = 4.18$; $p < .05$; Table 3.4 and Figure 3.3.4). When the bird was 75–84 cm away from the target object at the start of its approach, the object was in the bird's monocular field for a significantly longer proportion of the trial time than the binocular field (Tukey: $p < .01$). Then along the bird's approach from 74 to 24 cm, the object was in the bird's binocular field for a significantly longer proportion of the trial time than the monocular field (Tukey: all $p < .05$). Finally, from 24 to 5 cm, until it was within grasping distance, the target object was again in the monocular field for a significantly longer proportion of the trial time than the binocular field (Tukey: 15–24 cm, $p < .05$; 5–14 cm, $p < .01$).

Table 3.4 – A repeated measures one-way ANOVA table for the effect of distance (in cm) of the parrot from the target object on the proportion of time the object was in the monocular field (versus binocular field) in Experiment 2. Distance was a categorical variable (5-14, 15-24, 25-34, 35-44, 45-54, 55-64, 65-74 and 75-84 cm). The proportional data was arcsine-squareroot transformed.

Source	d.f.	SS	MS	*F*	*p*
Distance	**7**	**1116.1**	**159.4**	**4.18**	**0.031**
Error	2	305.0	38.1	214.61	< .001
Total	15	1421.1		116.79	< .001

Significant variable is indicated in bold; $n = 16$ for all measurements. Post-hoc Tukey: all $p < .05$.

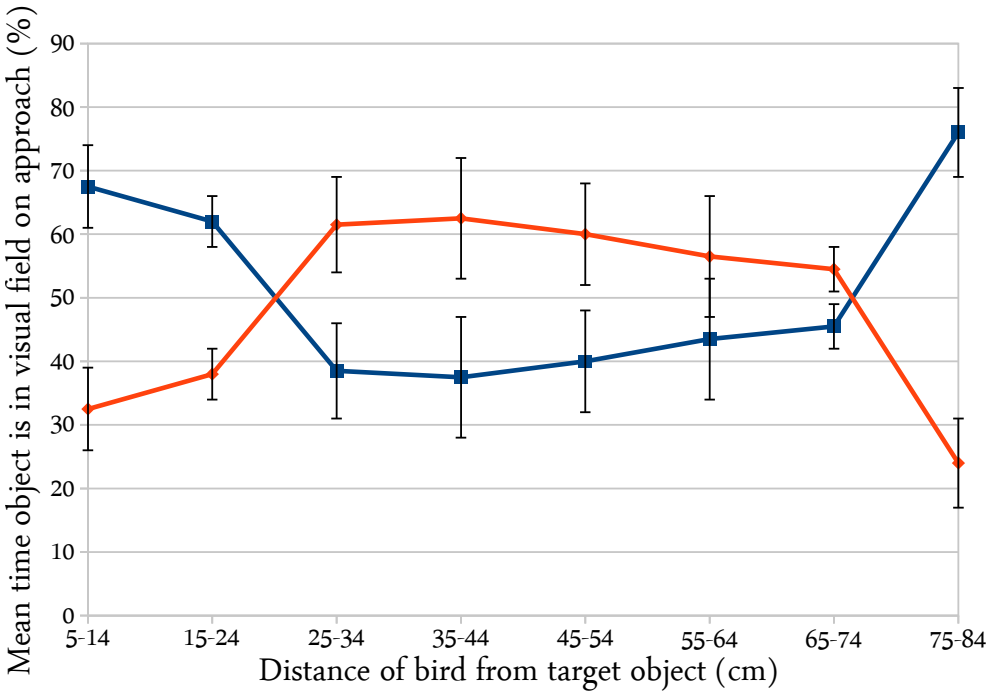


Figure 3.3.4 – A line graph illustrating how on a Senegal parrot's walking approach (Experiment 2), the visual field portion the object is in changes as the parrot gets closer to the object. The visual field portion was divided into the binocular field (red line) and the monocular field (blue line; either left or right). The distance the bird is from the object was categorised into 10 cm blocks. The approach finished once the bird was within grasping distance of the object (at 5 cm). The error bars represent the standard-error-of-the-mean, where the mean was across all the test conditions (object height varied), where two birds experienced three repeats of each condition.

3.4 Discussion

We have examined the orientation of the visual field during climbing and walking in parrots. Previous work in birds has focussed almost exclusively on head orientation during flight (Warrick et al., 2002; Tobalske, 2007), or just the locomotory mode of flight (Norberg, 1979; Heppner and Anderson, 1985; Bonser and Rayner, 1996; Zeffer and Norberg, 2003; Tobalske, 2004). The role of visual fields in climbing and walking is a previously understudied area for animals, although the locomotory aspects have been studied, largely in primates (e.g. Cartmill, 1985; Bonser, 1999; Preuschoft, 2002; Isler, 2003; Thorpe et al., 2007b; Manduell et al., 2011).

We found that whether a Senegal parrot is climbing or walking, as they approach a target object, they generally keep the object in their visual field near the point of maximum binocular width (forward and above the bird's head). This point also happens to be on the same plane as the point of maximum visual acuity (Demery et al., 2011). Even when they need to re-orient their head during climbing to use their bill as a third locomoting appendage, the target object is still in the parrot's visual field, but no longer near the point of maximum binocular width. In approach, they also predominantly orient their heads so that the object is in the frontal binocular portion of their visual field, rather than in one of the lateral monocular portions. As predicted, head orientation seemed to be dependent upon maintaining visual control, while body orientation seemed to be dependent upon maintaining vestibular control. Note that our target object was a food item, a mealworm, not a novel item, so extensions to exploratory behaviour can only be taken so far.

3.4.1 Climbing approach

The first experiment investigated the distinctive psittacine climbing mode of locomotion. For shallow inclines, the birds predominantly used their feet to climb, with the bill being used occasionally. As the gradient increased, the bill was used more frequently, until the bird was alternating use of foot and bill, rung by rung. While walking, only the feet were needed for locomotion, as there is no useful or necessary point for the bill to grasp.

When the bill was used to grasp supports in climbing, parrots oriented their heads downwards, so that the target object was near the periphery of the visual field, and the visual field was instead centred on the current (or next) point of contact for the bill, near the point of maximum binocular width. Nonetheless, because of the large binocular extent of 190º (Demery et al., 2011), the target object was still in the visual field (Figure 3.3.2). This seems to form part of a behavioural cycle in which the bird switches between fixating on these two points, depending on where they are along the supporting surface. As hypothesised, we found that the head angle was independent of the body angle, which was naturally dependent on the gradient of the supporting surface.

Contrary to our head angle findings, Green (1998) found that, while walking, chicks' head angle was dependent on the supporting surface gradient, i.e. to maintain vestibular control. Unlike in this study, however, he did not measure body angle, or consider whether the chicks were instead striving to maintain visual control of the distant target object of interest (caged conspecific). This could not be confirmed without knowing the visual field orientation of the species, which has not yet been measured. It is likely to be

very different to the psittacine visual field, as parrots inhabit very different environments to chickens (Martin, 2011). Moreover, when faced with a steep supporting surface, chickens do not climb as parrots do with their bill.

Nonetheless, Green's findings do to some extent support our body angle findings, where as the slope increased, the body angle also increased. Unlike our head angle results, this is likely due to the birds striving to maintain balance in the face of steeper inclines. However, an advantage of Green (1998) was that the head angles of chicks' descending as well as ascending different slopes were measured, increasing ecological validity. It is unfortunate there is not more known about how parrots move around in the wild. For example, whether they always climb by traversing along long branches, or whether parrots move between branches and change direction frequently. We chose to focus on travel in a single direction without any obstacles between the bird and the target object. This was in the interest of maximising control over knowing where the object was in a bird's visual field at any given moment in the approach, rather than solely investigating how parrots locomote.

One study that has investigated some of the details of parrot climbing is that by Zeffer and Norberg (2003). How the parrots legs have evolved to enable this form of locomotion efficiently is unclear, but Zeffer and Norberg (2003) found that the tarsus (lower leg) is significantly shorter compared to several other bird species. They suggested this allows for faster movement through the canopy, and the stability required for perching with one leg during extractive foraging. Williams and Bunkley-Williams (2012) studied the Puerto Rican spindalis (*Spindalis portoricensis*) moving through the canopy. These birds employ a very different means of climbing locomotion to par-

rots, whereby they swing from vine to vine by grasping them in their bill, rather than using their wings or feet.

One other possible concern with our method is that the target object was in the centre of the ladder rung, in line with the travel direction of the bird (like in Martin and Shaw, 2010). Therefore, we cannot be sure that the subjects were focussing on the object, rather than an some other distant point in their direction of travel, such as for identifying the next point of contact. If we were to repeat this study, it would be useful to, re-position the target object, for instance, to one of the extreme sides of the rung, away from the direct line of sight in the direction of travel. However, then we would need to work in more than one plane, so we would need to be careful when determining the relevant angles.

3.4.2 Walking approach

The second experiment focussed on the walking approach to a target object along a flat surface, where the height of the object was varied. In line with our predictions, the parrots' body angle remained constant throughout the approach, at approximately 50^{o} relative to the supporting surface. As the target object rose higher from the ground, the head angle relative to the supporting surface increased, probably because the parrot tracked the object as it moved towards it. Without the need to employ the bill in this mode of locomotion, the parrots oriented their heads throughout nearly all of their approach, so that the target object was near the point of maximum binocular width in the visual field.

These findings support Warrick and colleagues' (2002) work on how pi-

geons in flight maintain a clear view of what is in front of them by orienting their head independently of their body. In their experiments, the pigeon's body orientation and flapping frequency varied, but the head remained level in the direction of the destination throughout. When Warrick et al. disrupted the pigeon's visual and vestibular systems, it could no longer maintain controlled flight. Moreover, Cronin et al. (2005) looked at whooping cranes' locomotion during foraging. The cranes bob their heads as they walk, enabling them to keep a steady visual field for detecting and identifying objects. Furthermore, they maintained a speed that ensured their head was stable for at least 50% of the gait.

On the walking approach, the target object was predominantly in the Senegal parrots' frontal binocular field. The monocular fields of the parrots seemed to be important as well, but only at the beginning and the end of the approach. We suggest this is because the parrots first identify the target object laterally in the larger monocular field, which likely has a greater resolution than the binocular field (Martin, 2009).

Then visual control seems to be passed frontally to the binocular field on approach. This is an interesting consideration, as the psittacine binocular field only has a maximum width of 27° at the horizontal, relative to the 186° in one of the monocular fields (Demery et al., 2011). Nonetheless, while many other birds have even narrower binocular fields, in flight they have been shown to orient their head such that the frontal binocular field is in the direction of travel (Martin and Katzir, 1999; Martin and Shaw, 2010). It has been suggested that the avian binocular field is more suited to processing optical flow information than the monocular field (Martin, 2009).

Lastly, once the object is within grasping distance of the parrot, visual control appears to be transferred back to the higher resolution monocular field, and the next phase of exploration, exploratory manipulation, can take place. We look for evidence of this being the case in the next chapter.

We end this discussion with the observation that as we orientated the camera downwards, we could only measure where the object was in the visual field at the horizontal plane (as in Demery et al., 2011). We approximated that the extent of the visual field was simply that at the vertical midpoint. This is a reasonable approximation, as the field does not change greatly with height in this region. For example, the binocular width is $25^o \pm 2^o$ over a 160^o of the total 190^o of the binocular extent. However, extreme vertical head motion would not be accounted for. Without further advancement in eye-tracking technology though, this method is sufficiently accurate for measuring where different objects are in the bird's visual field at any given moment.

3.4.3 Summary

In this study we have discovered an interesting relationship between vision and the locomotory approach towards an object of interest, which has important implications for our understanding of how information may be gathered by exploration during different modes of locomotion. Parrots are distinctive for their locomotory modes and their visual field: both are closely intertwined, yet do not seem to hamper each other in the approach towards an object.

The psittacine bill is clearly a very versatile tool – for locomotion, tactile perception and manipulation. Unlike primates, climbing parrots have eyes

that are rigidly coupled to a key climbing appendage. There must be an evolutionary trade-off between between collecting information about distant objects and needing to look where to grasp next. It is still unclear whether psittacine visual fields are orientated – with extensive visual coverage above and behind the head – largely due to selection pressures pertaining to their characteristic climbing gait. While the findings in this chapter do support this view, we argue that as the object is in the visual field regardless of what gait is utilised, this orientation has evolved primarily due to the haptic perception afforded by the bill tip organ. For a social animal like the parrot, selection pressures are often particularly strong from threats posed by conspecifics and predators (Bertram, 1978). The bill tip organ allows parrots to forgo visual coverage of the region below the bill, such as for object manipulation, in favour of comprehensive visual coverage of above and behind the head, undoubtedly for greater detection of predators and conspecifics approaching from above or behind (Demery et al., 2011).

When the target object was in one of the monocular fields during the walking approach, we found both Senegal parrots displayed a preference for using their right monocular field of view more than than their left monocular. This issue of visual lateralisation has gained renewed interest in the literature of late, particularly in psittacines (Friedmann and Davis, 1938; Harris, 1989; Snyder and Harris, 1997; Casey, 2005; Rogers, 1989; Magat and Brown, 2009; Brown and Magat, 2011a). While the sample size of two birds in this study is sufficient for investigating the role of visual fields in locomotion following our current line of questioning, it is not adequate for investigating the possibility of individual versus population level visual lateralisation. Therefore, in the next chapter, we will re-examine the roles of the monocular and

binocular visual fields during exploration in another parrot species using a greater sample size, and we will relate the degree of visual lateralisation to the potential of ipsilateral* motor lateralisation (i.e. footedness). This will allow us to take a more haptic, rather than visual, stand-point in considering the next phase of exploration: exploratory manipulation.

CHAPTER 4

Haptic exploration in manipulation

How does an exploratory animal's senses and appendages interact to gather information from the world around it? While much work on animal exploration has focussed on the cognitive mechanisms underlying learning, comparatively little research has addressed the way in which the sensorimotor system may be designed to facilitate information acquisition. In addition, any information gathered by vision and touch during exploration may be constrained by cerebral lateralisation. Visual and motor lateralisation has been studied extensively in birds, but largely in foraging contexts, or with familiar (rather than novel) objects. Parrots are neophilic and exploratory throughout their lives and have the anatomy adapted for dextrous manipulation. Here we combined our knowledge of the psittacine visual field (Demery et al., 2011) with a novel technique to measure how kakariki utilise their eyes, bill and feet in the approach towards and in the manipulation of a range of novel objects. We found that on approach to an object, the binocular field was important, but once within grasping distance, the monocular fields dominated. Moreover, during this manipulation phase, the bill was used intensively for exploration. Unlike other psittacines measured to date, kakariki displayed not population-level, but strong individual-level visual and motor lateralisation. These different sensorimotor strategies are influenced by object novelty, the point at which the individual is in during the exploratory bout, and the types of exploratory behaviours being performed. Thus, it seems that the sensorimotor system of kakariki may be structured in such a way as to maximise the information gathered.

4.1 Introduction

TO survive within an ever-changing world, many animals need to explore. Exploration enables animals to learn about and understand the world around them (Archer and Birke, 1983; Renner, 1990). However, while most work has focussed on the cognitive mechanisms underpinning learning (e.g. Rescorla, 1968; Seed and Call, 2008; Bunzeck et al., 2010), learning relies on information gathered through the senses as raw material, and requires action through the motor system (Floreano and Mattiussi, 2008). Therefore, in order to understand learning fully, the focus needs to shift to the lower-level sensorimotor [1⋆] adaptations. How do different animals interact with their environments to gather information for exploration?

Studying exploration is complicated by the fact that the sensorimotor requirements and adaptations of a mole rat (*Spalax ehrenbergi*) exploring its underground environment, for instance, are very different to those of a octopus (*Octopus vulgaris*) exploring its underwater environment (Kuba et al., 2006a; Avni et al., 2008). We need to understand the extent of a species' perceptual and physical interaction with its environment before we can gain an insight into what types of information are being gathered by exploration. Moreover, it is not enough for the animal to just passively see or hear the world around it; to understand how it works, the animal needs to perform active and tactile interaction with the world (Piaget, 1929, 1952). An actively sensing animal is actively seeking and gathering information; it is being purposeful, exerting control over the orientation and direction of the sensory apparatus depend-

[1]It should be noted that, strictly, information gathered through the senses and that processed through the motor system are separate entities. As it is generally difficult to separate these two facets, particularly in behavioural experiments, henceforth we shall refer to both as sensorimotor.

ing on the task at hand to maximise the information gained (e.g. Mitchinson et al., 2007). In contrast, passive sensing involves simply receiving information from a source extrinsic to the individual – the difference between reaching out to touch something, in contrast to be being touched by something (i.e. sensor versus object movement, Gibson, 1962). Passive sensing is particularly difficult to measure because rarely involves overt behavioural changes in the animal, which makes it difficult for us to detect it and disentangle it from active sensing. Both forms of sensing often occur concurrently, sometimes through different modalities (Nelson and MacIver, 2006).

Active sensing is perhaps most evident in the modality of touch, where purposeful exploratory behaviour can be more clearly observed when the animal directs its haptic senses by movement and motoric action on the environment (Prescott et al., 2011). However, we cannot explicitly test whether an animal is actively using a particular sensory modality at a specific moment simply by observing exploratory behaviour. Nevertheless, we can deduce where a target object falls within a particular sensory modality at a specific moment. From there, it can be shown whether it is *possible* that the animal is using that particular modality to perceive that object at that moment (Chappell et al., 2012; Arriola-Rios et al., 2013). If we consider the animal's distinct senses (e.g. vision, touch) separately, we can then begin to distinguish between the respective passive and active forms, leading to insight into how the different types of information may be integrated by the brain into a single representation of the world (e.g. Mesulam, 1998; O'Regan and Noe, 2001).

Studying visual and haptic exploration has been addressed in greater depth in the human and robotic cognition literature. Indeed, proper motor

development and haptic exploration* is seen as integral to a human's effective understanding of the world around them (e.g. Gibson and Walker, 1984; Bushnell and Boudreau, 1993; Lederman and Klatzky, 1993; von Hofsten and Rosander, 2007; Turvey and Carello, 2011). Here we define haptic exploration as any information gathered passively or actively through inputs from receptors embedded in the skin (i.e. 'touch'), and/or in the muscles, tendons and joints (i.e. 'proprioception'* such as through grasping, e.g. see Lederman and Klatzky, 1993; Smith et al., 2009; Schneider et al., 2011). Moreover, human neuropsychology studies have revealed how object representations from one sensory modality are often finely interwoven with other sensory modalities (e.g. Alaerts et al., 2009; Schneider et al., 2011). Historically, developmental psychology has inspired many artificial intelligence researchers. This has led to some elegant, working models for exploratory 'baby' robots, which can effectively learn affordances* through object manipulation (e.g. Haruno et al., 2001; Natale et al., 2007; Kraft et al., 2010; Detry et al., 2010; Santana et al., 2010). The further advantage of investigating exploration in robots is that we know exactly what type of sensorimotor information the robot's 'brain' is receiving (Demery et al., 2010; Arriola-Rios et al., 2013).

Chappell et al. (2012) raised the question of how visual and haptic senses interact in non-human animals to gather information in different environments. The few studies that have paid attention to sensorimotor explanations of exploratory learning have done so in an evolutionary context of comparing different great apes species' cognitive development to that of humans (e.g. Parker and Gibson, 1977; Bard, 1995; Leca et al., 2011). Poti and Spinozzi (1994) investigated locomotion and prehension development in different great ape species by utilising techniques from human developmental

psychology. This study found that the more precocious the locomotion development within a species, the more primary their mode of environmental interaction. This in turn meant the greater the hindrance for them to fully understand the physics of the world. For instance, unlike chimpanzees (*Pan troglodytes*), babies cannot start to locomote quadrupedally towards objects until 8–9 months, when they have already started to understand spatial and causal relations between multiple objects, through varying fine exploratory actions on objects, thus producing various environmental effects (e.g. sound or movement from banging or pushing an object).

Beyond the great apes, other studies have described the specific sensorimotor and related neural anatomy of various species. For example, echolocation in brown bats (*Eptesicus fuscus*, Ulanovsky and Moss, 2007), magnetic perception in zebra finches (*Taeniopygia guttata*, Keary and Bischof, 2012), and chemosensing in planktonic shrimp (*Acetes sibogae australis*, Hamner and Hamner, 1977). However, few have described these impressive sensorimotor adaptations in a behavioural context, such as in observing how different appendages interact during exploration, presumably to gather environmental information (e.g. cephalopod molluscs in Grasso and Basil, 2009). The little research there is suggests many species do display active information-gathering, where the form of different animals' sensorimotor behaviour is formed in such a way as to allows greater information quality and quantity. For instance, in utilising both behavioural and robotic techniques, it has been shown rats (*Rattus norvegicus*) alter their whisking behaviour* pattern and speed to increase information about object shape and texture gained through their vibrissae* (Grant et al., 2009; Prescott et al., 2009). Blind cave fish (*Anoptichthys jordani*) detect environmental features by combining their own swim-

ming movements with their mechanosensory lateral line system (Weissert and Campenhausen, 1981). In novel environments, they vary their swimming velocity according to what they detect, thus increasing the efficiency of perceiving the mechanosensory cues (Teyke, 1988; Hassan, 1989).

Interactions between the motor and sensory systems may constrain the ways in which animals can gain information from their environment. Cerebral lateralisation*has been extensively studied in birds. This is where the division of the two brain hemispheres often manifests itself as side biases in motor behaviour (e.g. 'handedness/footedness'*), or in a preference for stimulus perception on the left or right side (Rogers, 2002). Although not specifically considered in this context to date, studying lateralisation may prove useful in considering how it may be constraining, or, perhaps, informing an animal's senses and appendages interacting to gather information about the world. For instance, if a bird is right-side lateralised, then it would hold a novel object in its right foot, and may only view the object with its right eye. From this, we can begin to reason what types of information may be available to the bird, once lateralisation has taken place.

Until relatively recently cerebral lateralisation was thought to be unique to humans because of its links to language and other 'complex' cognitive processes (e.g. Crow et al., 1998). However, the chicken (*Gallus gallus*) has proved a particularly useful experimental model for showing otherwise (Rogers, 1995). Avian lateralisation is triggered during incubation, leading to behavioural asymmetries (Rogers and Sink, 1988). For instance the left eye is used more in spatial learning (e.g. Regolin et al., 2004), while the right eye dominates in times of neophobia or flight responses (e.g. Vallortigara and

Andrew, 1994). New Caledonian crows (*Corvus moneduloides*) also exhibit lateralisation (both visually and motorically) in their use and manufacture of tools. This is at the individual rather than population level – that is to say individual birds display a preference for one side or the other, but there is an even split between birds as to which side is preferred (Hunt et al., 2001; Weir et al., 2004). However, to our knowledge, no one has yet looked for evidence of lateralisation during exploration.

Often the avian hemispheres process and store information quite independently of each other, and many species show a large amplitude of independent eye movement (Rogers, 2000, 2002; Voss and Bischof, 2009). This has interesting cognitive and behavioural implications (e.g. in food-caching birds, Clayton and Krebs, 1994). It is thought that, depending on the type of information required for collection, the monocular fields provide greater resolution than the binocular field, particularly close to the target of interest (Martin, 2007). The binocular field is probably better suited for detecting movement, or for processing the optic flow-field* information produced while locomoting (Martin, 2009). However, the evolutionary function of the monocular versus binocular visual fields is still an area of much debate (e.g. Fernandez-Juricic et al., 2010; Troscianko et al., 2012) and only with behavioural research can we draw any further conclusions. Thus, study of the exploratory approach to and manipulation of an object could be particularly revealing.

Parrots present a particularly compelling case for investigating how their sensorimotor system is structured to maximise the information gathered from the environment by exploratory learning. They are often generalist extractive

foragers and live in dynamic habitats, where environmental information frequently changes and novel problems often present themselves (Collar, 1997; Rowley, 1997). These selection pressures favour higher exploratory activity, flexible learning mechanisms and sensorimotor adaptations for gathering information about a wide variety of novel objects. Indeed, parrots have a great exploratory dexterity at manipulating objects and they often display neophilic, innovative behaviour for investigating novel items (Smith, 1971, 1975; Whittow and Sturkie, 1999; Luescher, 2006). For example, wild kea (*Nestor notabilis*) innovate novel techniques to attain food in artificial situations, such as opening complex restaurant bin lids (Gajdon et al., 2006; Huber and Gajdon, 2006).

Parrots accomplish these feats with a very distinctive motor apparatus, utilising zygodactyl* feet, a muscular tongue and a hook-like bill joined to the skull by a synovial joint* (Homberger, 1980; Zweers and Berkhoudt, 1994; Tokita, 2004). Sigerson (1888) called the parrot bill the 'third prehensile organ', with independently moving upper and lower jaws. Moreover, where other birds peck at food, parrots have been described to chew food like ruminants with their thumb-like shaped tongue, aided by the support of a foot (Smith, 1971). Unlike other zygodactyl birds that climb vertical trunks (e.g. woodpeckers, Piciformes), parrots' feet may instead be adapted for secure grasping of branches (Bock and Miller, 1959). This evolutionary adaptation may have improved object manipulation with feet, which may have improved extractive foraging. We suggest that in tandem with parrots' highly investigative nature, it may have also allowed for better object exploration.

Furthermore, the psittacine sensory apparatus is very intriguing. With

independently moving eyes placed high and laterally in the skull, psittacines have both a relatively broad frontal binocular field and an extensive field of view above and behind their head (Demery et al., 2011, chapter 2). It is thought this allows them to travel efficiently in the direction of an object of interest and observe it at close range, while remaining vigilant for predators (chapter 3). This visual orientation has further been attributed to the haptic perception afforded by their bill tip organ, which is unlike that described in any other bird species to date (Goujon, 1869; Demery et al., 2011). Touch does seem to be a very important sensory modality for exploring psittacines, as the somatosensory* area in their brain is highly developed (Stingelin, 1965; Wild, 1981; Wild et al., 1997; Sultan, 2005; Gutierrez-Ibanez et al., 2009). However, to date, few behavioural experiments have investigated how these different senses and motor adaptations may interact to enable efficient exploration in the parrot's environment.

Parrots' motor dexterity has led to them becoming a focus for the lateralisation literature, particularly as a unique animal model for human handedness. Snyder and Bonner (2001) found that like human infants (e.g. Kampmer et al., 1985), African Grey parrot chicks (*Psittacus erithacus*) undergo a delayed development of motor lateralisation, prior to adequately developed autonomous motor and thermoregulatory controls – an evolutionarily adaptive strategy for altricial animals. Other studies have described strong foot preferences in parrots, but have largely only presented parrots with opportunities to manipulate food items, rather than novel objects (Friedmann and Davis, 1938; Harris, 1989; Snyder and Harris, 1997). Psittacine eye preferences have been described in conjunction with this apparent motor lateralisation by Brown and Magat (2009; 2011a), but the methods used relied on

a judgement of which eye was the dominant one in fixating on a food item. This judgement was decided during live observation, rather than from video analysis, based upon the side to which the bird cocked its head towards the food item (C. Brown, personal communications). Our study of parrot visual fields has shown (Demery et al., 2011) that it is difficult to make live judgements about which eye is fixating on an object. This is particularly pertinent given parrot visual fields have:

1. an encompassing monocular field;

2. a relatively large degree of overlap between the monocular fields;

3. and an even larger degree of non-conjugate eye movement.

In chapter 3, we utilised a different, more accurate method for measuring eye preference, or at least approximately where the 'target object' was in a Senegal parrot's (*Poicephalus senegalus*) visual field at any given moment. Note that we cannot know for certain where in the surrounding environment the parrot is focussing without more invasive techniques. This experiment only used two subjects and did not measure how parrots orientate their heads once they are within grasping distance of the object, when exploratory manipulation can commence, nor how this apparent visual lateralisation may relate to any motor lateralisation. To date, no study has considered psittacine visual *and* motor lateralisation in the context of manipulating and exploring novel objects. Moreover, while these previous lateralisation studies have investigated how the feet are involved in manipulation, none have considered how the parrot's bill may contribute to this manipulation, particularly for gathering haptic information about the environment.

The structure of the parrot's visual field (orientated above the head) and somatosensory importance of the bill and feet suggests the exploration process should be divided into two phases: exploratory approach* and exploratory manipulation*. Parrots can only use (passive) vision while out of reach of the object, but we propose that they will use active sensing using the bill and feet to explore the object once it is within their reach. This chapter outlines how we integrated our knowledge of the psittacine visual field (Demery et al., 2011) with a novel video analysis technique (chapter 3) to measure how kakariki (*Cyanoramphus novaezelandiae*) utilise their eyes, bill and feet in the exploratory approach towards and in the exploratory manipulation of a series of familiar and novel objects. Specifically, we aimed to follow three lines of investigation:

1. how visual control of an object is passed between the monocular and binocular fields on a kakariki's approach towards it;
2. how the bill and feet interact at different stages of exploratory manipulation of an object;
3. how visual and motor lateralisation exhibited through eye and foot preferences play a role in constraining the exploratory manipulation of an object.

Kakariki, or New Zealand red-fronted parakeets, are especially social, neophilic and active compared to other psittacines (Pepperberg and Funk, 2005), which makes them an ideal species for studying exploration. They show high levels of dexterity in manipulating objects, and they use the same method of extracting seeds as found in nearly all Psittaciformes (Collar, 1997). Kakariki can be found at all strata of temperate rainforests, but they are also resident

to scrub and grassland habitats. They have a highly generalist diet, largely consisting of seeds, fruit, leaves, buds, flowers, shoots, and nectar, but also insects, animal remains, tiny stones, as well as seaweed and mussels in coastal areas (Greene, 1988, 1998; Funk and Matteson, 2004; Kearvell et al., 2002). They mature at approximately 9 months and live for 5–10 years.

Following our first aim, we measured which portion of the visual field the target object is in, on a kakariki's exploratory approach to it. Senegal parrots were shown to orientate their heads so that the target object was in a monocular visual field at the beginning and the end of a walking approach towards it (chapter 3). However, in between these two points, the object was largely in the *binocular* field of view. In this previous study, the target object was a familiar food item, so in the current study we also asked whether object novelty would influence which part of the visual field its in. Perhaps when a novel object is present, information is needed more quickly, so the greater resolution afforded by the monocular field would supersede the need for an efficient approach afforded by the binocular field with optic flow.Thus, on exploratory approach we predict that:

- the proportion of time the object is in a monocular or the binocular field will vary with distance from the object, such that;
  - the object is first identified in one of the monocular fields;
  - then for the main part of the approach, the object is maintained in the binocular field;
  - once the parrot is within grasping distance of the object, it is largely maintained in one of the monocular fields again.
- whether the object is novel or familiar will have a significant effect on

the proportion of time the object is held in a monocular or the binocular field.

Two key sets of appendages that allow the kakariki interact with its environment are the feet and the bill (including the tongue). During the exploratory manipulation phase, both sets may play both a sensory role, utilising touch, proprioception and taste, and a motor role, as dextrous manipulators. We can only directly observe the motor role and, from that, infer about the sensory role. The relative exploration time with the bill versus one of the feet may provide an insight into which appendage is more important/adapted for gathering information and exploratory learning, and which provides more of a supporting role. However, respective appendage usage may vary over the exploratory bout and with object novelty. For instance, it may prove adaptive to keep a novel object as far away from body (and particularly the head) as possible until the affordances and potential risks are better understood. There is anecdotal evidence that juvenile kea (*Nestor notabilis*), another New Zealand psittacine, first reach out with one of their feet when presented with a novel object, before full manipulatory object play* commences (Diamond and Bond, 1999).

Frequently, it is challenging to discriminate between information-gathering exploratory behaviour and executive action. When picking up an object, an animal may either singularly, or in parallel, be wanting to transport it, or/and gain information about its weight (e.g. Elner and Hughes, 1978). So in conjunction with measuring sensorimotor adaptations, we should record the type of exploratory behaviour being performed on an object. This will clearly have an impact on the type of appendage usage, as illustrated in the

description of object play in macaques (*Macaca mulatta*; Power, 2000). This leads us to our second set of hypotheses, regarding relative appendage usage during the exploratory manipulation phase:

- overall, the bill will be used for a greater proportion of manipulatory time compared to either of the feet;
- early in an exploration bout, the feet will be utilised for a longer ;
- for novel objects, the feet will be employed as the manipulatory appendage more frequently;
- the choice of appendage usage will be affected by the type of exploratory behaviour performed on the object and whether the target object is familiar or novel.

Following our last line of investigation into how lateralisation may constrain or inform kakariki exploratory manipulation, we again turn to the Senegal parrot experiments for both hypotheses and methods (chapter 3). There, the preliminary results indicate we will find a population level of visual lateralisation in kakariki, where the object will be in the right monocular more than the left monocular field. For the majority of other parrot species, the right foot appears to be the dominant foot for manipulation (Harris, 1989; Snyder and Harris, 1997; Snyder and Bonner, 2001; Brown and Magat, 2011b), occurring on the ipsilateral* side to the preferred eye (Magat and Brown, 2009; Brown and Magat, 2011a).

As with appendage usage, it is important to investigate how the form of exploratory behaviour being performed and object novelty may influence the degree of visual and motor lateralisation. Chickens prefer different sides ac-

cording to what type of behaviour they are performing (e.g. feeding versus flight), revealing underlying hemispheric specialisation (e.g. Vallortigara and Andrew, 1994; Regolin et al., 2004). A fish, the blue gourami (*Trichogaster trichopterus*) has been shown to visually and motorically prefer the left while exploring (Bisazza et al., 2001), but detail beyond these general behavioural categories is not known. In a related, but separate, finding on object novelty, the small-eared bush baby (*Otolemur garnettii*) switches eye preferences depending on whether it is viewing a familiar or a novel object (Rogers et al., 1994). The authors argue this reflects an adaptive response to a potentially threatening stimulus, increasing the arousal level, which is commonly associated with right-brain function. Consequently, our last set of hypotheses on exploratory manipulation are that:

- the object will appear for a greater proportion of time in the kakariki's right eye monocular field of view than the left monocular field;
- the kakariki will manipulate the object for a greater proportion of time with the right foot rather than the left;
- both of the previous predictions will depend upon the type of the exploratory behaviour employed and whether the object is novel or familiar.

4.2 Methods

4.2.1 Subjects and housing

The subjects were 20 kakariki (*Cyanoramphus novaezelandiae*; 10 females; 10 males). They were parent-raised and were sourced from four different breeders in the United Kingdom, so they were probably hybrids with the yellow-

fronted parakeet (*C. auriceps*; Boon et al., 2001). Six of the birds were raised within our captive laboratory environment (all hatched in April – May 2010). Once the chicks were 6 months of age, they were transferred to other cages. The other 14 birds were delivered from the breeders when they were 3 months of age, then quarantined for 28 days (all hatched April – May 2008).

The kakariki were housed indoors according to guidelines set out in Hawkins et al. (2001) and Kalmar et al. (2007; 2010). They were kept in a temperature-controlled environment (23 ± 5ºC) on a 12:12 light cycle (dark from 8 pm to 8 am daily; UV daylight light bulbs with a high flicker frequency). The kakariki were housed in pairs in adjoining aluminium cages, each sized 1.83 x 1.22 x 1.22 m. They were cleaned out weekly and fed daily at 11 am on a diet of fresh fruit and vegetables with a parrot seed mix (Parrot Mix Royale, Copdock Mill, Ipswich, UK). Wood chips (Lillico Biotechnology, Surrey, UK), water baths and a range of toys and ropes were provided for general environmental enrichment. However, due to another study, half of the kakariki were housed in a more enriched room, while the other 10 were housed in a less enriched room (chapter 5).

4.2.2 Video sampling

The data for this chapter was sampled from video recordings of a range of exploratory behaviour tests conducted between March 2009 and April 2012. The familiarity of the target object in each video was recorded, where 'familiar' was defined as the subject having experienced the target object at least once in a previous trial and 'novel' as when they had not.

Three videos were analysed for each individual, one from each year. Note

that for the seven kakariki hatched in Spring 2010, the third video was selected pseudo-randomly, from either their first or their second year. Each individual never entered into more than one trial each day. The date selected for each video for each individual was pseudo-randomised, with the constraint that across individuals there were an equal number of trials occurring in the morning and afternoon. This method of date selection determined that the type of behavioural test being performed and whether the target object/apparatus was familiar or novel at that sampled date was pseudo-randomised. Despite this, there was an approximately equal number of trials (from all individuals) across the different behavioural tests and an equal number of trials with a novel object and a familiar object, so there was no overall bias in the dataset.

During a trial, when an individual was performing a non-exploratory behaviour (e.g. maintenance behaviour; see ethogram in Appendix C) for more than 30 seconds, or the bird was out-of-sight of the camera (i.e. climbed cage side/ceiling), the video was fast-forwarded until that non-exploratory bout ended or the bird came back into view. The image frames from this non-exploratory bout were then excluded from the analysis. If this resulted in an individual with significantly fewer total analysed frames compared to the other individuals (chi-square goodness-of-fit test), then another video was randomly selected and analysed.

In each frame, the data about the location of the object in the subject's visual field obtained from the video was combined with the data recorded live about object novelty, appendage usage and exploration behaviour category (subsection 4.2.3).

4.2.3 General behavioural tests protocol

The behavioural tests investigated how different object properties influence the pattern of exploration for a separate study (chapter 6). While the general protocol was consistent across tests, the test object varied between tests (Figure 4.2.1). None of the work conducted for this project required a Home Office Licence and all the techniques used were non-invasive, following the guidelines set out by the UK Animals (Scientific Procedures) Act, 1986.

The test object was set up on a table within a custom-made test cage (67 x 58 x 60 cm) before the subject entered the test room. The experimenter sat on the other side of a solid screen in front of the apparatus to avoid visual cueing. The subjects' behaviour was monitored remotely and recorded via two video cameras (Sanyo Xacti VPC-CG10, recorded using MPEG-1/2 codec, 720x576 resolution, 30 fps) positioned perpendicular to the test cage, above and to the side of it. Both cameras covered the entire table area within the test cage, but not all of the sides and ceiling of the cage. There was a habituation period of five minutes, then the trial lasted 25 minutes.

Immediately before each behavioural experiments' test trials, the kakariki first experienced three habituation trials with a familiar piece of rope over consecutive days (similar to that in their home cage). The general protocol for the habituation trials was the same as the test trials. The time of day that each individual was moved to the test room was pseudo-randomised between 0900 and 1700 between days. The kakariki were trained to individually enter and exit a portable transport cage (81 x 42 x 61 cm), by means of a food reward (strawberry). To ensure that the birds' attention was drawn to the link between entering/exiting the cage and the reward a clicking sound

Figure 4.2.1 – Illustrations of all of the test objects.

(produced by a standard dog training device) was employed to seize their attention. When, infrequently, a net was required to catch the bird, an extra five minutes of habituation was allowed in the test room.

All of the ensuing behaviours were recorded live via remote monitoring, according to the ethogram described in Appendix C, using JWatcher Video version 1.0 (Blumstein et al., 2007). The five main exploratory behaviour categories were:

- visual inspection (e.g. follow, search);
- grasping (transitory e.g. tap; or prolonged e.g. carry);
- actions (e.g. push, pull);

- modifying objects (e.g. bend, pry);
- relating objects (e.g. insert, hook).

A subject's exploration of a target object was divided into two phases based on its distance from the object: the 'exploratory approach phase'* from 70 cm to within grasping distance (bird and object 5 cm apart); and the 'exploratory manipulation phase'* when the target was within grasping distance. These two phases formed the basis for three key analyses as outlined in the following three subsections:

1. binocular and monocular visual field usage during exploratory approach;
2. different appendages usage during exploratory manipulation;
3. visual and motor lateralisation during exploratory manipulation.

4.2.4 Exploratory approach: binocular and monocular visual field analysis

Firstly, we investigated whether object novelty and distance to the object affected binocular versus monocular field usage. The key measure for this analysis was the mean proportion of exploratory approach time the object was in either the monocular or binocular visual field. This mean was calculated for each of the 20 kakariki across three test trials.

Using the well-established ophthalmoscopic reflex technique (Martin, 2007), but with the bird held in hand, we verified that the following key features of the kakariki visual field were the same as those found in Senegal parrots (Demery et al., 2011):

1. the frontal binocular field extended vertically to include the projection of the eye-bill tip direction in its lower periphery;
2. the binocular field extended vertically through approximately 180° so that there was no blind area directly above the head and near comprehensive visual coverage of the frontal hemisphere;
3. and maximum binocular width was approximately 20° and this width extended throughout a large sector of the field above and below the horizontal plane.

We concluded that the visual fields of kakariki and Senegal parrots are substantially similar and that the characteristics of the visual field of Senegal parrots could be used to investigate the use of vision in exploratory behaviour in both species. Thus, virtually the same method of frame-by-frame analysis employed in chapter 3 for Senegal parrots was used with kakariki from the videos sampled (subsection 4.2.2). This analysis determined whether, at any one moment on a walking exploratory approach to a target object, the object (i.e. test apparatus) was in binocular field, or one of the monocular fields.

We modelled our analysis method on that of Cronin et al. (2005). The video files were converted into an image sequence (unscaled JPEG, with interlaced scaling and no compression) using MPEG Streamclip version 1.2 (Cinque, Squared 5srl 2006-08), so a 25-minute 30 fps video file would result in approximately 45,000 image frames. ImageJ (v. 1.43u 64-bit; Wayne Rasband, National Institute of Health, USA) was used for frame-by-frame analysis every 30 frames per second, working *backwards* from the first point of bill contact with the target object. This meant that in total a maximum of 90,000 frames were processed. This level of sampling was selected by a pilot

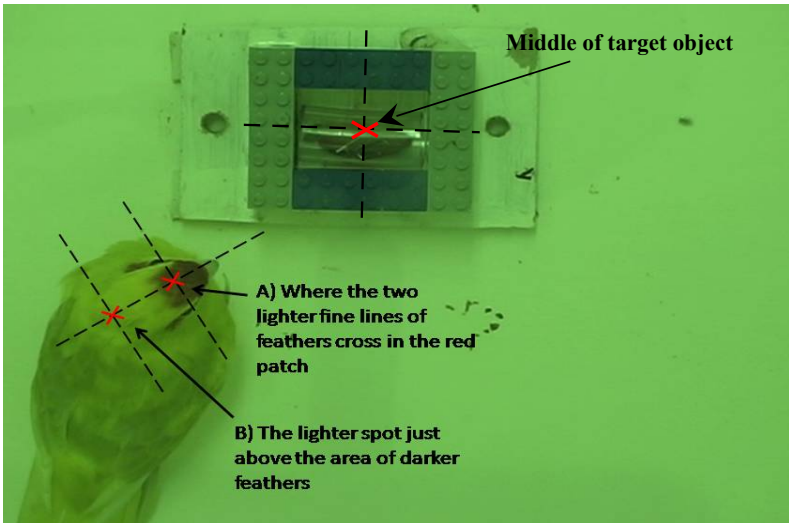
study, which tested different sampling intervals to check which was sufficient to extract the information required. The following points in the image frames from this video footage were marked (Figure 4.2.2a):

- a consistent point on the back of the head (e.g. white spot in feathering);
- the mid-point between the eyes;
- and the middle of the mealworm.

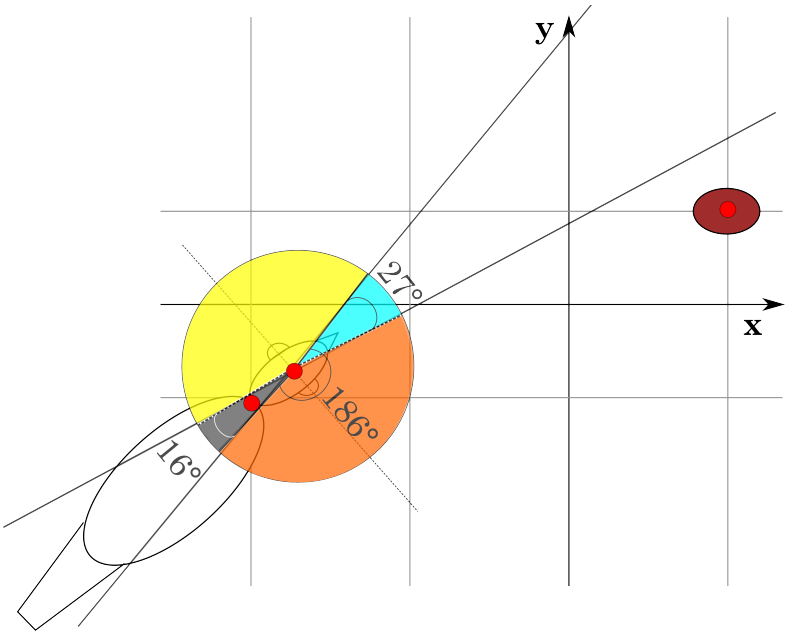
These points were chosen so that the general position of the object in the visual field at any given moment could be calculated by trigonometry (Appendix B). These trigonometry calculations thus made the following assumptions:

- take a top-down, two-dimensional view of the bird in relation to the object along the x, y-axes (Figure 4.2.2b), so discount any head movements along the z-axis for instance;
- assume the bird always orientates its head to focus on the item of interest in the plane/elevation of maximum binocularity (as shown in Demery et al., 2011);
- and assume that the eye is looking in the 'average direction', but there will an error of ± 20^{o} due to non-conjugate eye movement.

Within a trial, an exploratory approach was only included in the analysis if the first walking approach a bird makes towards an object (whether novel or familiar) was from over 15 cm away. If the trigonometry calculations (Appendix B) showed the object was not in the visual field in particular frames (e.g. if too far behind the bird's head), then these frames were excluded from the overall statistical analysis. If this process resulted in an individual with



(a)



(b)

Figure 4.2.2 – The key points (red crosses and dots) for analysing a kakariki's exploratory approach towards a test object, recorded by a video camera positioned above and perpendicular to the test object. These points were chosen so that the position of the object in the kakariki visual field at any given moment could be calculated by trigonometry. Firstly, **(a)** shows the three specific points in an example image frame from the video: (A) was the mid-point between the eyes; (B) was a consistent point on the back of the head; and (C) was the centre of the target object or test apparatus. Note point (B) was consistent within individuals, but may vary slightly between individuals. These points could then be related to the behaviour the bird was performing at that time and the distance they were from the target object. Secondly, **(b)** illustrates how the kakariki visual field was effectively superimposed over each of these frames to determine whether the object was in left monocular (yellow), right monocular (orange), or binocular field (blue). The circle represents a section through the bird's visual field in the plane that passes through the eye and the bill tip (50° below the horizontal, as in Demery et al., 2011). The dark grey area is the blind area. The details of the trigonometry calculations (from the x, y co-ordinates of each point) are shown in Appendix B.

significantly fewer total analysed frames compared to the other individuals, then another video was randomly selected and analysed. In considering the binocular field versus monocular field within this analysis, we did not distinguish between the left and right monocular fields.

The effect of distance from the object on the visual field orientation on approach was also analysed. Distance was grouped into six categories of 10 cm. Distance analysis ended when the object was within 5 cm of the bird (grasping distance).

4.2.5 Exploratory manipulation: type of appendage usage analysis

Secondly, we investigated which appendages were key during exploratory manipulation (i.e. haptic exploration). The key measure for this was analysis was the mean proportion of haptic exploration time within one trial, when the object was either being manipulated by the bill, one of the feet or another body part. This mean was calculated for each of the 20 kakariki across three test trials. We further analysed whether object novelty and when this exploration occurred during the trial affected this measure. Moreover, we investigated whether the type of exploratory behaviour affected appendage usage, but by utilising a slightly different measure – the mean proportion of each exploratory behaviour category's frequency within a trial spent using each appendage type.

Thus, the frame-by-frame analysis from subsection 4.2.4 continued into the next exploration phase. During this exploratory manipulation phase, each frame was linked with what exploratory behaviour was being performed at the moment from the live data recorded in JWatcher (subsection 4.2.3).

This live recording included data on which appendages were being used (bill/left foot/right foot/other body part/combination) with each exploratory behaviour.

A pilot study revealed that the bill was rarely used in isolation (Z. P. Demery and J. Chappell 2010, personal observations). However, the bill was often used together with one of the feet, where while a foot held an object up to the bill, the bill performed more complex exploratory manipulations on the object (e.g. mouthing, see Appendix C). For analysis in these cases, the bill was defined as the primary appendage and the foot as the secondary appendage. Note that both appendages may still be providing both sensory information (whether active or passive) and motor support. One of the feet was defined as the primary appendage when it was used in isolation from the bill. Appendage usage was analysed over the trial time, where the trial time was divided into five 5-minute blocks.

4.2.6 Exploratory manipulation: visual and motor lateralisation analysis

Thirdly, we investigated whether the kakariki had individual level or population level visual and motor lateralisation. Then if so, whether these eye and foot preferences were found on ipsilateral or contralateral sides; and whether object novelty had an effect on these preferences. The key measure for this was the mean proportion of time when the object was in each monocular field and in each foot during the exploratory manipulation phase within a trial. This mean was calculated for each of the 20 kakariki across three test trials.

Thus, from the data gathered in subsection 4.2.4 and subsection 4.2.5, for each subject during exploratory manipulation we could determine if:

1. the object was in the left monocular field or the right monocular field for a greater proportion of the exploratory manipulation time;
2. and the object was manipulated in the left or right foot for a greater proportion of the exploratory manipulation time.

If the object was in one of the monocular fields significantly longer than the other, then the kakariki would be said to be 'visually lateralised'. Similarly, if the object was manipulated or acted on more with one foot than the other, then the kakariki would be said to be 'motor lateralised', or to display 'footedness'. Whereas, if the object was in either monocular field or each foot for a nearly equal proportion time, then the kakariki would be said to be 'ambidextrous'. This data formed the basis of our population-level analysis on visual and motor lateralisation. We looked at whether there was a significant difference between the number of individuals that were left lateralised and the number of individuals that were right lateralised.

Furthermore, we ran an individual-level analysis on visual and motor lateralisation. To analyse whether each kakariki was lateralised (rather than ambidextrous), a score independent of the direction of laterality was needed. In other words, the level of deviation from 'ambidexterity'; an established method, as in Brown and Magat (2011b). This was calculated by subtracting 50% from the percentage of time the object was in the left side (i.e. the absolute value minus 50). The individual was defined as being lateralised – or 'strongly lateralised' to one side or the other – if the magnitude of the score

was over 10. An individual with a maximum score of 50 was completely lateralised (e.g. 100% time used right hand), but an individual with a score of 0 was completely ambidextrous (50% time left side, 50% time right side). Each individual's mean score was calculated from three trials. We then compared the number of individuals that were lateralised (scoring 11–50) to those that were not (scoring 0–10).

Frames where the object was in the binocular field, or in the bill alone (thus effectively out-of-sight) were excluded from the visual and motor lateralisation analyses. The side used both visually and motorically for each type of exploratory behaviour could be determined from the data gathered in subsection 4.2.3. At the individual-level, we also analysed which side each bird used in the case of novel objects, familiar objects and overall. We classed each bird as either favouring left or right eye/foot for each category, and then tested which of these three cases (if any) were dependent on each other. Any ambidextrous birds were not included in this object novelty analysis.

4.2.7 Statistical methods

For the type of appendage analysis and the binocular and monocular visual field analysis, effects were analysed using a repeated measures General Linear Model. The assumptions of parametric methods (normality of error, homogeneity of variance and linearity) were confirmed from plots of coefficients versus fitted values. As all of the measures used proportional data, the data was arcsine-squareroot transformed. All analyses were performed using Minitab® Statistical Software version 15.1.30. The probability level accepted for significance was $p < .05$.

The assumption of normality was not met for the proportion of exploration time measure in the appendage usage analysis, so chi-square goodness-of-fit tests were run instead. Similarly, all of the visual and motor lateralisation analyses were performed using chi-square goodness-of-fit tests.

In all of the models, the following factors were also included to check whether they had an effect on the key measures: sex, age, origin (i.e. breeder or cage hatched in), cage number and the total number of frames analysed for each individual. As the general key measures were means for each of the 20 kakariki across three test trials (see last three subsections above), a series of unpaired *t*-tests were performed on each individual, to check whether the time, date or the test type of the sampled video had an effect on the proportion of time spent exploring.

4.3 Results

There were no significant effects found for sex, age, origin total number of frames analysed, home cage number, experiment type, time or date of test on any of the key measures.

4.3.1 Exploratory approach: binocular and monocular visual fields

Proportion of approach time with distance

During the exploratory approach phase, the distance the kakariki was from the target object had a significant effect on the proportion of the approach time the object was in the binocular field (as opposed to one of the monocular fields; GLM: $F_{5,105} = 51.82$, $p < .001$; Table 4.1). As Figure 4.3.1 shows, when the bird was 55–64 cm away from the target object at the start of its approach,

Table 4.1 – A summary table outlining the two repeated measures GLM model for the effect of distance (of the kakariki from the target object) and the effect of object novelty on the proportion of time the object was in the binocular (versus monocular) field during the exploratory approach. For both models, the proportional time data was arcsine-squareroot transformed. Sex and cage number (1 – 7) were included in both models as fixed factors, while age and the total number of frames analysed were included as covariates. Distance (5-14, 15-24, 25-34, 35-44, 45-54 and 55-64 cm) and object novelty (familiar or novel) were fixed factors for their respective models.

Factor	**d.f.**	***F***	***p***
Distance$^{\diamondsuit}$	**5**	**51.82**	**< .001**
Sex	1	0.58	0.449
Cage no.	6	0.70	0.650
Age	1	0.00	0.980
Analysed frames	1	0.16	0.686
Object novelty$^{\sun}$	1	0.49	0.491
Sex	1	2.02	0.166
Cage no.	6	1.27	0.299
Age	1	0.07	0.792
Analysed frames	1	0.67	0.421

Significant variables are indicated in bold. $^{\diamondsuit}n = 120$; post-hoc Tukey on distance effect: all $p < .05$. $^{\sun}n = 40$.

the object was in the bird's monocular field for a significantly longer proportion of the trial time than the binocular field (Tukey: $p < .01$). Then along the bird's approach from 54 to 25 cm, the object was in the bird's binocular field for a significantly longer proportion of the trial time than the monocular field (Tukey: all $p < .05$). Finally, from 24 to 5 cm, until it was within grasping distance, the target object was again in the monocular field for a significantly longer proportion of the trial time than the binocular field (Tukey: 15–24 cm, $p < .05$; 5–14 cm, $p < .01$).

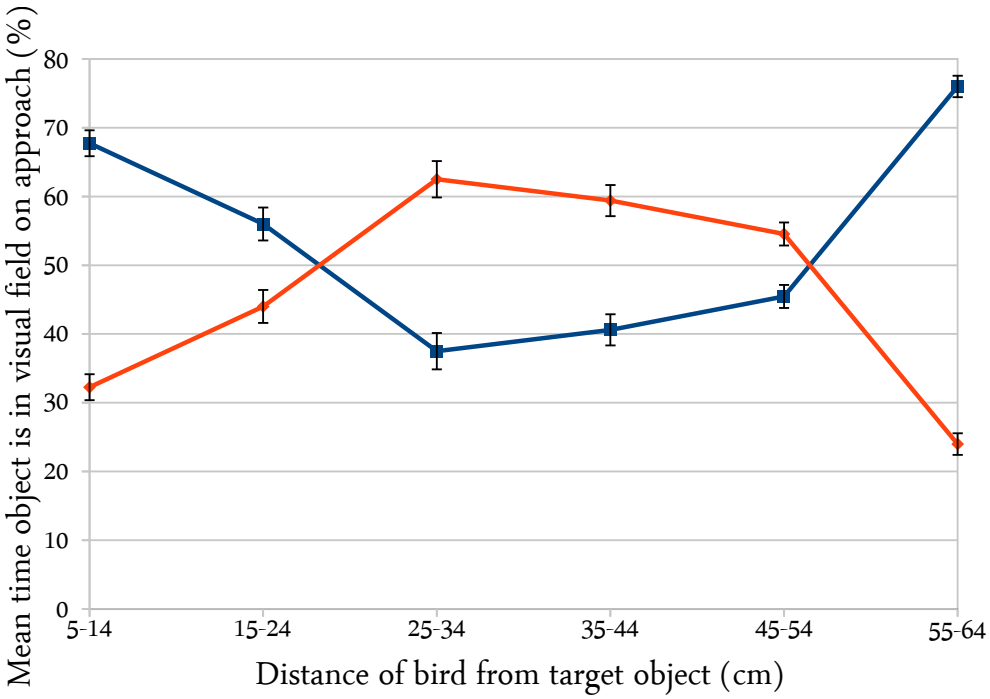


Figure 4.3.1 – A line graph illustrating how on a kakariki's exploratory approach, the visual field portion the object is in changes as the kakariki gets closer to the object. The visual field portion was divided into the binocular field (red line) and the monocular field (blue line; either left or right). The distance the bird is from the object was categorised into 10 cm blocks. The exploratory approach within a trial was defined as having occurred if the first walking approach a bird makes towards an object (novel/familiar) was from over 15 cm away. The approach then was finished once the bird was within grasping distance of the object (at 5 cm). This data was based on each of the 20 kakariki's mean across three test trials. Only two trials were discarded for not having approaches, but not all of the analysed approaches were across the entire distance available (maximum 64 cm). The error bars reflect the standard-error-of-the-mean.

Object novelty

Object novelty had no significant effect on the proportion of time the object was in the binocular field on exploratory approach (GLM: $F_{1,29} = 0.49$; $p > .05$; Table 4.1).

4.3.2 Exploratory manipulation: type of appendage usage

Proportion of exploratory manipulation time

During the exploratory manipulation phase, there was a significant difference in the proportion of haptic exploration time within one trial when the object was being primarily manipulated by either the bill, one of the feet of another body part (chi-square goodness-of-fit test: χ^2 = 612.23, d.f. = 1, n = 1930.09; $p < .001$; Table 4.2). As Figure 4.3.2 shows, overall the bill was used as the primary appendage in manipulation (or in isolation) more than the feet (left or right) or any other body part (e.g. wing). See subsection 4.3.3 below for whether there was an effect of left or right foot. As other body parts were used so rarely across trials for exploratory manipulation (mean 2.5 ± 1.85 % of trial), so they were not considered for any other statistical analyses.

Object novelty and when exploration occurred during a trial

There was significant effect of trial time on when the bill (as opposed to either foot) was being utilised as the primary manipulatory appendage (GLM: $F_{4,172}$ = 788.75; $p < .001$; Table 4.3). Additionally, whether the trial contained a novel object or not had a significant effect on appendage usage (GLM: $F_{1,172}$ = 34.94; $p < .001$). A significant interaction was found between these two factors (GLM: $F_{4,172}$ = 4.15; $p < .01$).

Post-hoc tests indicated one or both feet were used significantly more than the bill in the first 10 minutes of a trial (Tukey: $p < .01$), especially when the target object was novel as opposed to familiar (Tukey: $p < .01$). As shown in Figure 4.3.3 though, in the last 15 minutes of a trial, the bill was used increasingly more than the feet (Tukey: $p < .01$). Note there was no significant

Table 4.2 – A chi-square goodness-of-fit test was performed on the proportion of haptic exploration time within one trial to test whether the object was being primarily manipulated by either the bill, one of the feet, or another body part during the exploratory manipulation phase. This proportional time data was arcsine-squareroot transformed.

Category	Observed	Test Proportion	Expected	Contribution to χ^2
Foot	734.77	0.333	643.364	12.987
Bill	1034.33	0.333	643.364	237.581
Other	160.99	0.333	643.364	361.661

$\chi^2 = 612.23, d.f. = 1, n = 1930.09, p < .001$

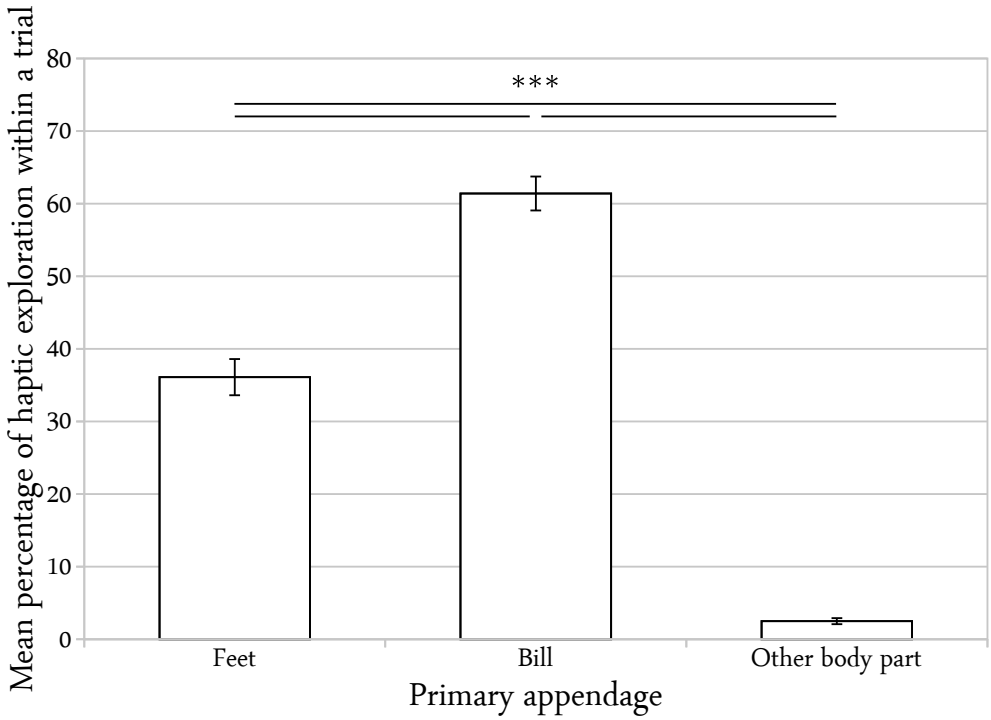


Figure 4.3.2 – A bar chart illustrating the percentage of haptic exploration time within one trial when the object was being primarily manipulated by the bill, one of the feet, and another body part. There were 20 kakariki (*Cyanoramphus novaezelandiae*) altogether and this data was based on each bird's mean across three test trials. One trial lasted on approximately 25 minutes. The error bars reflect the standard-error-of-the-mean. The lines over the each pair of bars indicates a significant difference between that pair at $p < .001$ (***; chi-square goodness-of-fit).

Table 4.3 – A summary table outlining the two GLM models for effects of object novelty and trial time (i.e. when exploration occurred during a trial) on the proportion of haptic exploration time using bill (versus feet) and the effect of exploratory behaviour category on the proportion of exploratory behaviour frequency, all during the exploratory manipulation phase. All of this proportional data was arcsine-squareroot transformed. Sex, cage number (1 – 7) and origin (10 levels, either breeder or cage ID) were included in both models as fixed factors, while age and the total number of frames analysed were included as covariates. Object novelty (familiar or novel) and trial time (0-5, 6-10, 11-15, 16-20 and 21-25 minutes) were fixed factors in the first model and behaviour category (transitory grasping, prolonged grasping, actions, modifying objects and relating objects) was a fixed factor in the second model.

	Factor	**d.f.**	***F***	***p***
% haptic exploration time using bill$^{\diamondsuit}$	**Object novelty**	**1**	**34.94**	**< .001**
	Trial time	**4**	**788.75**	**< .001**
	Sex	1	0.15	0.703
	Cage no.	6	1.82	0.097
	Origin	9	0.99	0.449
	Age	**1**	**4.73**	**0.031**
	Analysed frames	1	0.17	0.685
	Object novelty × Trial time	**4**	**4.15**	**0.003**
% exploratory behaviour frequency$^{\sphericalangle}$	**Behaviour category**	**4**	**72.38**	**< .001**
	Sex	1	0.23	0.631
	Cage no.	6	0.87	0.518
	Age	1	0.31	0.578
	Analysed frames	1	0.35	0.558

Significant variables are indicated in bold. $^{\diamondsuit}n = 199$ $^{\sphericalangle}n = 99$

interaction of object novelty with appendage usage in the last 15 minutes of the trial (Tukey: $p > .05$).

Exploratory behaviour type

As illustrated in Figure 4.3.4, there was a significant effect of the behaviour category on the proportion of exploratory behaviours utilising the bill (rather than the feet) as the primary appendage (GLM: $F_{4,86} = 72.38$; $p < .001$; Table 4.3). Post-hoc tests indicated the bill was used significantly more for transitory grasping behaviours (e.g. mouthing, tapping, probing), whereas the feet

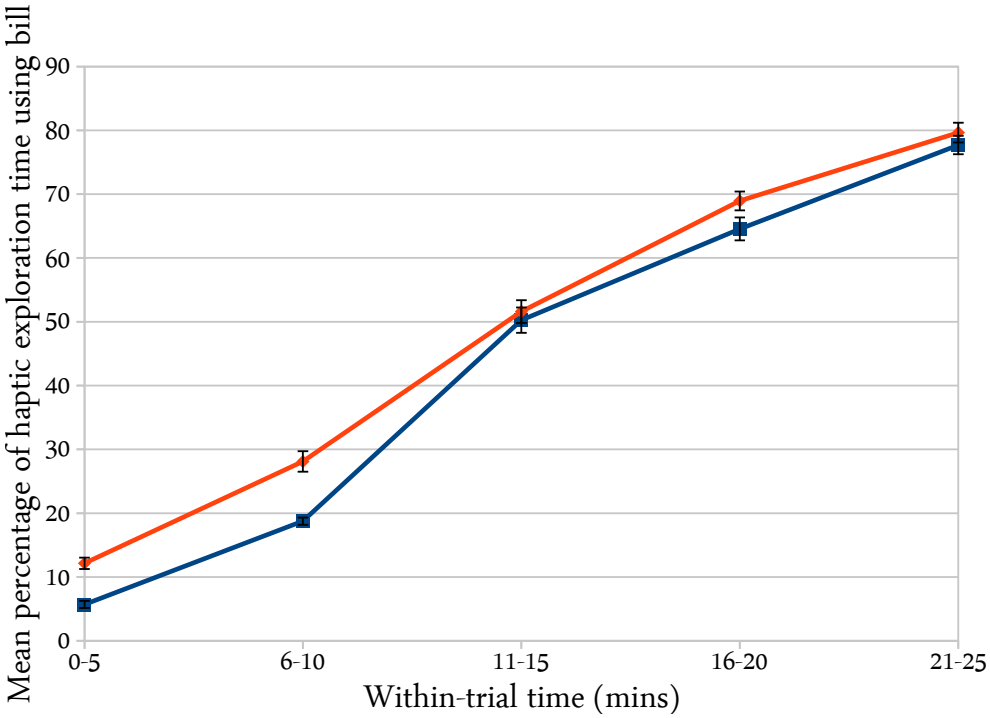


Figure 4.3.3 – A line graph illustrating the interaction between object novelty and kakariki's (*C. novaezelandiae*) primary appendage usage over trial time (maximum 25 minutes). There were 20 kakariki altogether and this data was based on each bird's mean across three test trials. The error bars reflect the standard-error-of-the-mean. When two appendages were used together, the primary appendage was defined as the the appendage (out of the bill, or left or right or foot) that performed the more complex object manipulations, while the secondary appendage played a supporting role. Specifically, primary appendage usage is displayed here as the percentage of haptic exploration within a trial spent using the bill. A 'familiar' (red line) object was defined as the bird having experienced the object at least once in a previous trial and 'novel' (blue line) was when they had not. The within-trial time was categorised into 5-minute groups. Object novelty only had a significant effect in the first 10 minutes of a trial (Tukey: $p < .01$).

were used more for prolonged grasping behaviours (e.g. holding, carrying, transferring etc.; Tukey: $p < .001$). Moreover, the bill was used more during behaviours involving object modifications (e.g. extract, hook, arrange etc.) and, to a lesser extent, object relations (e.g. bend, squeeze, pry etc.; Tukey: $p < .001$). However, the feet were used more for actions relying only on a single object (e.g. push, rotate, throw etc.; Tukey: $p < .001$).

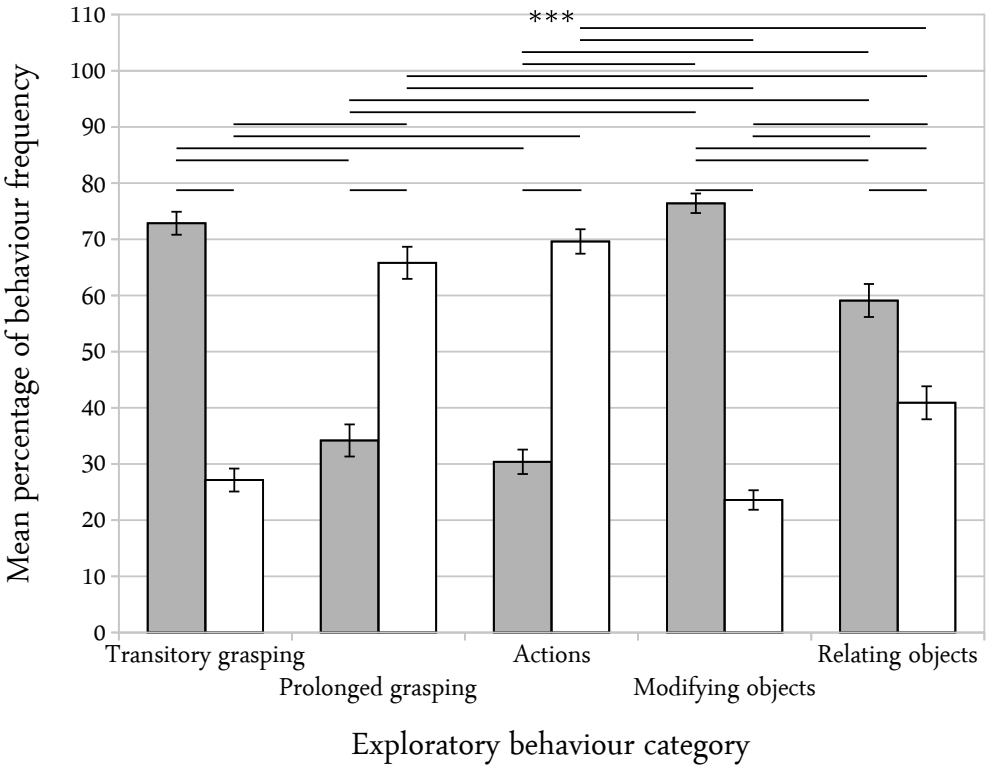


Figure 4.3.4 – A bar chart illustrating the relative appendage usage by kakariki in different exploratory behaviour categories. This was measured as the percentage of each behaviour category's frequencies within a trial (25 minutes) spent using either the bill (grey) or one of the feet (white). For the ethogram detailing each category, see Appendix C. There were 20 kakariki altogether and this data was based on each bird's mean across three test trials. The error bars reflect the standard-error-of-the-mean. The lines over each pair of bars indicates a significant difference between that pair at $p < .001$ (***; Tukey).

4.3.3 Exploratory manipulation: visual and motor lateralisation

Individual or population level effects

At the population level, there was no significant difference between the number of kakariki that had the object in the left monocular field for a greater proportion of exploratory manipulation time (within trial, as opposed to the right monocular field) than the number of kakariki that had the object in the right monocular field for a greater proportion of time (chi-square goodness-of-fit test: $\chi^2 = 0.80$, d.f. $= 1$, $n = 20$; $p > .05$; Figure 4.3.5a and Table 4.4). Simil-

Table 4.4 – A series of chi-square goodness-of-fit tests were performed to test for individual and population level effects and object novelty effects on visual and motor lateralisation. numbers in brackets are their respective categories in observed values

Research question	Categories	χ^2	p
Population level visual lateralisation?	left (12) vs. right (8)	0.8	0.371
Population level motor lateralisation?	left (7) vs. right (13)	1.8	0.180
Individual level visual lateralisation?	**ambidextrous (4) vs. lateralised (16)**	**7.2**	**0.007**
Individual level motor lateralisation?	**ambidextrous (4) vs. lateralised (16)**	**7.2**	**0.007**
Preferred eye & foot on contralateral or ipsilateral sides?	**ipsilateral (4) vs. contralateral (17)**	**9.8**	**0.002**
Same eye for viewing novel & familiar objects?	**same (1) vs. different (19)**	**16.2**	**< .001**
Eye preferences same overall & for novel objects?	same (10) vs. different (10)	0	1.000
Eye preferences same overall & for familiar objects?	same (9) vs. different (11)	0.2	0.655
Same foot for grasping novel & familiar objects?	same (11) vs. different (10)	0.01	1.000

Significant effects are indicated in bold; for all measures $d.f. = 1$ and $n = 20$.

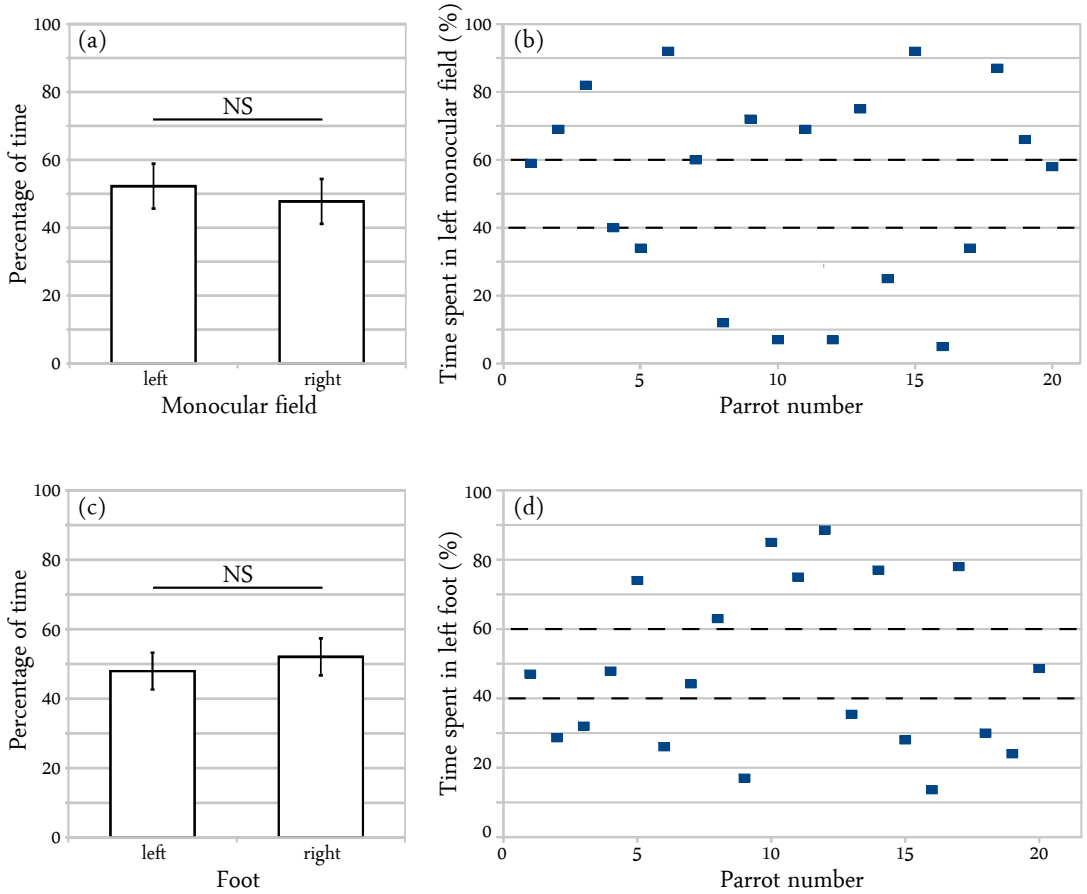


Figure 4.3.5 – Individual and population level analysis of visual **(a–b)** and motor lateralisation **(c–d)**. The bar charts in (a) and (c) show how there was no significant difference at the population level between the 20 kakariki (*C. novaezelandiae*) in preferring either the left or right eye/foot. This data was based on an individual's mean percentage of exploratory manipulation time the target object was in each monocular field (excluded when in binocular field), or each foot, within a trial (25 minutes). The individual's mean was calculated from three trials. The error bars reflect the standard-error-of-the-mean. The lines over the each pair of bars indicates there was no significant difference between that pair (hence 'NS'; Tukey, $p > .05$). However, the scatter plots in (b) and (d) shows individual kakariki did have a preference for one eye and for one foot over the other. The allocated parrot identity numbers are along the x-axis and the percentage of time the object was in the left side is along the y-axis. The area within the dotted lines shows the region of non-lateralisation ('ambidexterity'). So the individuals above the dotted region were left lateralised and the individuals below the dotted region were right lateralised.

arly, no population level motor lateralisation to one direction or another was found (from the proportion of time each foot was manipulating the target object; $\chi^2 = 1.80$, d.f. = 1, $n = 20$; $p > .05$; Figure 4.3.5c).

At the individual level, there were a significantly greater number of kakariki ($n = 16$) that were visually lateralised in one direction or another, than the number of 'ambidextrous' kakariki ($n = 4$), where the object was in the left or right monocular field for a relatively equal proportion of time (chi-square goodness-of-fit test: $\chi^2 = 7.20$, d.f. = 1, $n = 20$; $p < .01$; Figure 4.3.5b). Similarly, an individual level of motor lateralisation was found ($\chi^2 = 7.20$, d.f. = 1, $n = 20$; $p < .01$; Figure 4.3.5d).

There were significantly more kakariki ($n = 17$) where their eye preference was on the contralateral (opposite) side to their foot preference, than the number of kakariki where their eye preference was on the ipsilateral (same) side ($n = 3$) to their foot preference ($\chi^2 = 9.80$, d.f. = 1, $n = 20$; $p < .01$). If for instance, the dominant eye of a kakariki was the left eye, then the dominant foot would be the right foot.

Object novelty

We then ran an individual-level analysis on which eye the kakariki used for novel and familiar objects. There was a significantly greater number of kakariki ($n = 19$) where the object spent more time in different monocular fields for novel and familiar objects, rather than in the same monocular field (chi-square goodness-of-fit test: $\chi^2 = 16.20$, d.f. = 1, $n = 20$; $p < .001$; Figure 4.3.6 and Table 4.4).

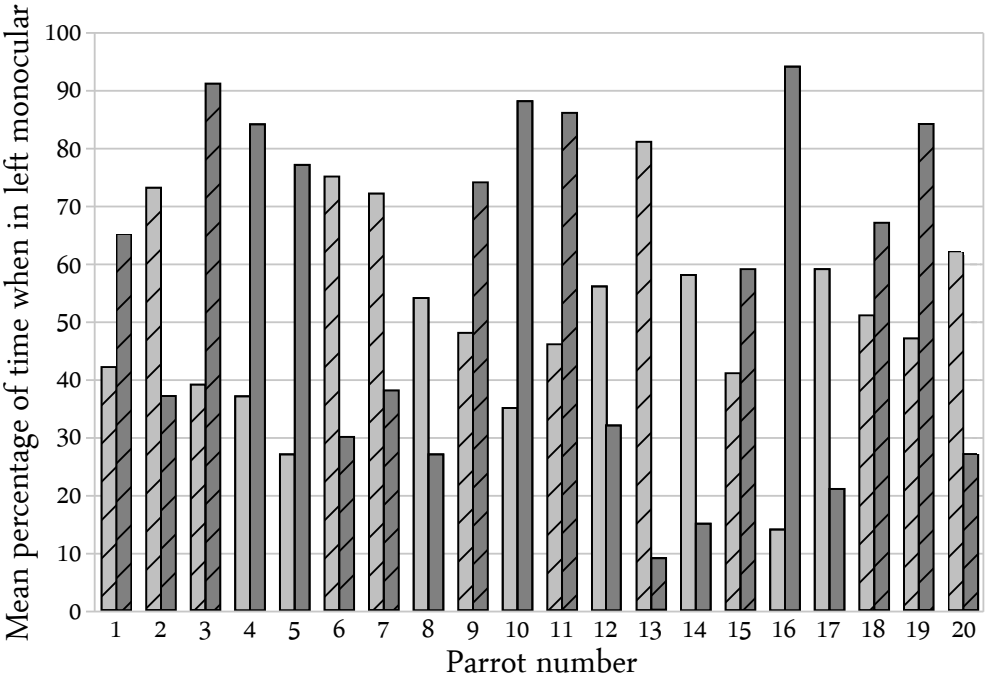


Figure 4.3.6 – Although there no population level effect was found, this bar chart illustrates how at the individual level, there was a preference for one of the monocular fields when viewing novel objects (in light grey), while the opposite monocular field was used for familiar objects (in dark grey) during the exploratory manipulation phase. Note the birds with the hatched bars are overall have a preference for the left eye (see also Figure 4.3.5b). This figure caption corresponds to that of Figure 4.3.5.

We then considered whether on an individual-level, the overall preferred monocular field was the same as the monocular field used for viewing novel versus familiar objects. No significant effect between these two factors was found, as approximately the same number of kakariki used the same or different monocular fields overall and with novel objects (χ^2 = 0.00, d.f. = 1, n = 20; $p > .05$). The same was found between overall field choice and familiar object field choice (χ^2 = 0.20, d.f. = 1, n = 20; $p > .05$).

Similar pair-wise chi-square goodness-of-fit tests found no significant effects for the preferred left or right foot with novel and familiar objects (all χ^2

= 0.01, d.f. = 1, $n = 20$; $p > .05$). Note the same tests found no significant effects found of exploratory behaviour type on either eye choice and foot choice (all $p > .05$).

4.4 Discussion

We have uncovered an interesting and relatively complex pattern in how the sensorimotor apparatus of parrots is adapted to support their exploration of their environment, both in their approach to and manipulation of the target object. On an exploratory approach, kakariki passed visual control of a target object between the monocular and binocular fields, but this varied with distance and object novelty as predicted. Subsequently, during the exploratory manipulation phase, the primary exploratory appendage of the kakariki appeared to be the bill. As hypothesised, this varied with the type of exploratory behaviour employed, whether the object was novel or not, and the stage of the exploration bout. For instance, the feet were used more frequently early on in a bout, especially when the target object was novel. We further revealed some interesting findings about kakariki lateralisation both visually and motorically, which to some extent contradicts previous work (particularly Magat and Brown, 2009; Brown and Magat, 2011a). As predicted, these were also influenced by object novelty to some degree. We would like to suggest that these sensorimotor adaptations are structured so that the kakariki can maximise the information gathered from the environment by exploratory learning.

4.4.1 Exploratory approach: binocular and monocular visual fields

There is a great debate about the evolutionary function of avian binocular and monocular fields, especially taking into account the distinctive neural

underpinnings (Rogers, 2000, 2002). Compared to other birds measured to date, parrots have a particularly large frontal binocular field and a large amplitude of independent eye movement (Demery et al., 2011). However, psittacine binocularity (maximum width 27°) does not approach the extent of primate binocularity (~145°; Martin, 2009), which allows for depth perception through stereopsis*. Moreover, the large amplitude of parrots' independent eye movements could abolish binocularity within a single saccade.

One explanation for differential use of the visual fields is that the monocular field in birds has greater resolution than the binocular field, which is more suited to detecting movement, or for processing the optic flow-field* information produced while moving (Martin, 2007, 2009). This supports our finding that on the approach towards a target object kakariki, like Senegal parrots (chapter 3), seemed to first identify the target object in one of the monocular fields, then transferred visual control to their binocular field as they began moving towards it. Then once they were within grasping distance of the object, they viewed it predominantly with one of the monocular fields again, presumably taking of advantage of the greater resolution afforded. At close range, this point is particularly salient, as the monocular fields are simply much larger than the binocular field (Demery et al., 2011). Parrots are extractive foragers and their bill tip organ, rather than their visual field, likely provides substantial haptic information to allow accurate control of items held within the bill. In other birds that do not need accurate control of their bill for foraging through vision, their binocular field is narrow (e.g. filter-feeding ducks; Martin, 1994).

One might predict that the monocular fields would continue to be used

more than the binocular during most of the exploratory manipulation phase. Parrots are often seen bringing food items or novel objects up into their field of view with their feet (Whittow and Sturkie, 1999; Luescher, 2006). However, we did not analyse this, due to the difficulties in determining whether an object is in the binocular field once grasped at close range, particularly if grasped by the bill. Alternative methods, such as the latest eye-tracking technologies, or more higher-resolution, synchronised cameras around the testing area may resolve these issues in the future (e.g. Kjaersgaard et al., 2008; Voss and Bischof, 2009).

Contrary to our hypotheses, we found no significant effect of object novelty on the object's position within the binocular and monocular fields on the approach to it. We reasoned that when a novel object was present during an exploratory approach, more information would be needed quicker, and the greater resolution afforded by the monocular field would supersede the need for an efficient approach afforded by the binocular field with optic flow. However, perhaps during this exploration phase, whether the viewed object is novel or familiar is simply irrelevant for efficient visual perception by optic flow while the bird is moving. It would have been interesting to see if novelty of the target object had an effect on which monocular field was utilised at the beginning and end of the approach. While we did investigate this issue in the exploratory manipulation phase, there were not enough frames for a comparison between phases. A much greater number of exploratory approaches would be needed in a future study.

Another issue with our method was that the frame-by-frame analysis did not incorporate a cluster analysis for checking for intra-observer reliability

between frames/trials and between subjects. There may also have been some in error in the feather movement between frames. However, as we were only interested in where the object fell in the visual field according to very broad categories (left or right monocular, binocular or blind area), any errors were unlikely to have altered the outcome.

4.4.2 Exploratory manipulation: type of appendage usage

The two key sets of appendages that are adapted to allow kakariki to interact with their environment are the zygodactyl feet and the hooked bill. Overall, we found the object spent a significantly greater proportion of the exploratory manipulation time in the bill, rather than in either of the feet. Both the bill and the feet may be able to supply detailed sensory input. However, from our behavioural data we can only *infer* what form of information each appendage may be gathering and thus we can only make educated suggestions about what role they each may be playing. Nonetheless, as the bill contains both the bill tip organ and the tongue, it is certainly able to provide more modes of sensory input than the feet. This, combined with its motor flexibility (the hooked shape, synovial joint and muscular tongue), may well explain why the feet in the exploratory manipulation phase appeared to provide a supporting role in securely holding the object up to the bill.

When each appendage was used, we found a significant difference between their relative proportion of frequencies performing different types of exploratory behaviours. The kakariki used the bill more for 'transitory grasping' behaviours (e.g. tapping or probing), while they used the feet more for 'prolonged grasping' behaviours (e.g. transferring or holding down). The argument for the bill being the prime exploratory appendage was further suppor-

ted by our finding that the bill was employed more than either of the feet for fine exploratory manipulations, involving object modifications or multiple objects. This may be due to the mechanoreceptors embedded in the hard keratin of the parrot's bill (Demery et al., 2011), combined with the similar receptors in the tongue, allowing perception of a wider range of stimuli, such as temperature, vibrations and different forms of pressure (Goujon, 1869; Necker, 1972; Gottschaldt and Lausmann, 1974; Berkhoudt, 1979; Gentle and Breward, 1986; Cunningham et al., 2007, 2010). Moreover, the relatively enlarged somatosensory area of the psittacine brain predominantly represents the bill and tongue over the feet (Stingelin, 1965; Wild, 1981; Wild et al., 1997; Sultan, 2005; Gutierrez-Ibanez et al., 2009).

In addition to its sensory role, the bill also plays a dextrous motor role; Sigerson (1888) called the parrot bill the 'third prehensile organ'. Indeed, in answer to Corballis (1983), Peters (1988) argued that the bill would be the main manipulatory organ, with the feet positioning the object so that the bill can better act on it. He thought it was analogous to the human left hand supporting the right hand in manipulation. Where other birds peck at food, parrots have been described to chew food like ruminants with their muscular tongue, again aided by the support of a foot (Smith, 1971).

A similar interaction between the roles of the hands and mouth is found in human infants (Bushnell and Boudreau, 1993). Before differentiated finger movements can develop under efficient visual control, 3-month-old infants can perform much more intricate movements on objects with their mouths and tongues, rather than their hands. One example of an oral sensorimotor exploratory behaviour is cyclic active sucking, which allows an infant

to learn about the hardness and texture of different objects (Rochat, 1987). An infant's hands appear to act simply as supports to these oral exploratory behaviours of the mouth/tongue (Gibson and Walker, 1984). There is unfortunately not much more evidence on the actual role of hands in these types of situations (Streri and Feron, 2005). Nonetheless, one cannot dispute that human hands become the dominant exploratory manipulatory appendages later on in life. While intriguing, we also need to be cautious about how far we can extrapolate from our knowledge about human sensorimotor adaptations to understand those of the kakariki.

We made the assumption that when the bird was using both the bill and feet to explore an object, that the feet were playing a mechanical/supportive role, in helping to position the object for manipulation by the bill, rather than a sensory role. This appears to be a reasonable assumption to make, as it is likely that the bill has richer sensory capabilities than feet (i.e. tongue, bill tip organ; e.g. Goujon, 1869; Wild et al., 1997; Sultan, 2005; Gutierrez-Ibanez et al., 2009). However, that is not to say that the feet are not also involved in gather information, particularly about the mass of the object and other mechanical properties (Wing and Lederman, 2009; Ferreira et al., 2010; Chappell et al., 2012). It difficult to disentangle the respective roles of the bill and feet when they are used together, without directly recording neural signals, but the bill is rarely used without the feet under natural conditions (Z. P. Demery and J. Chappell 2010, personal observations). It may be more prudent to consider appendage usage in exploratory manipulation as either a 'single-sensory stream', or 'multi-sensory streams' of information.

The kakariki used their feet more frequently than their bill while physic-

ally interacting with the target early on in their exploration bout, especially when the object was completely novel to them. Presumably this is because of the potential threat the object poses (e.g. toxic food item). However, as the individual gathers more information about it through tentative manipulation with the feet (which are less vulnerable body parts than the bill/tongue, and spatially separated from the eyes/head), familiarity increases. Hence later on in the exploration bout, the bill is employed more than the feet.

Similar results have been reported in another New Zealand parrot, the kea (Diamond and Bond, 1999). While this apparently supports our interpretation of the results, both species spend much of their lives foraging on the ground compared to other psittacines (Greene, 1998; Diamond and Bond, 1999). Hence these results may not be extendable to arboreal parrots, who may instead only use their feet later on in an exploratory bout, as foot manipulation brings the possibly threatening object close to the vulnerable body (C. Mettke-Hofmann, personal communications). In the future, it would be interesting to analyse appendage usage in more detail in relation to the types of exploratory behaviours typically exhibited throughout the exploration bout, particularly in other species.

4.4.3 Exploratory manipulation: visual and motor lateralisation

We know that, at least for kakariki, the object is mainly manipulated *within* the bill (Figure 4.3.2), where the visual field is limited (subsection 4.2.4). The visual field extends to only about 10° below the bill tip, and around the bill tip, the frontal binocular field is only approximately 10° wide, as opposed to approximately 27° at the horizontal (Demery et al., 2011). While out of reach of the object on approach, parrots can only use vision, but not touch. Once

within reach, although the bird can bring the object directly and closely up to either eye with one of its feet (and is often seen doing this; Z. P. Demery and J. Chappell 2010, personal observations), the lack of visual perception when the bill is manipulating the object again emphasises how vision is less important during the exploratory manipulation phase. Nonetheless, we found some intriguing visual lateralisation results, reflected to some extent in the motor lateralisation results. These findings are the first to our knowledge in the ornithological literature combining both modalities in an exploratory context, particularly in such detail.

We found evidence in kakariki of individual-level visual lateralisation during the exploratory manipulation phase. This did not extend to a population level. In other words, the kakariki were visually lateralised in preferring to view the object of interest with one particular monocular field rather than the other, but it varied from individual to individual whether this preferred monocular field was on the left or right side. A similar result has been found for New Caledonian crows when manufacturing or using tools; another cognitively flexible species inhabiting a dynamic environment (Hunt et al., 2001; Rutledge and Hunt, 2004; Weir et al., 2004). The individual, rather than population level laterality in both bird species may be due to perceptual biases, such as embryonic light exposure (Rogers and Sink, 1988), or retinal differences resulting in different neural outputs (Hart et al., 2000). Strong laterality at the individual level confers several selective advantages, including efficient foraging, complex motor tasks and increased cognitive performance (Rogers et al., 2004).

There was also an effect of object novelty at the individual level. When an

object was novel to the kakariki, they were more likely to use the opposite eye to that which they used to explore familiar objects. However, no significant effect was found for whether the overall preferred monocular field was the same as the monocular field used for viewing novel versus familiar objects. This is because approximately the same number of kakariki used the same or different monocular fields overall, as with novel objects. An increased sample size would likely give us more insight into this subtly complex relationship.

This effect of object novelty/familiarity on visual lateralisation has not been investigated in birds, but has to some extent in mammals. The small-eared bush baby (*Otolemur garnettii*) has been shown to switch eye preferences depending on whether it is viewing a familiar or a novel object (Rogers et al., 1994). The authors argue this reflects an adaptive response to a potentially threatening stimulus, increasing the arousal level, which is commonly associated with right-brain function. However, the sample size was relatively small and they were not presented with novel, neutral items (e.g. rope) as well as the novel, very fear-inducing objects (e.g. rubber snake). We moreover need to careful in applying any hemispheric specialisation explanation (e.g. Rogers, 2000, 2011) to kakariki, as different individuals had different side preferences for novel and familiar objects.

As hypothesised, the kakariki motor lateralisation findings reflected the visual lateralisation findings, but again only at the individual level. Also, counter both to our hypotheses and to the previous literature (e.g. Magat and Brown, 2009; Brown and Magat, 2011a), this motor lateralisation occurred on the contralateral side, rather than the ipsilateral side of the visual lateralisa-

tion. So, for instance, if a kakariki viewed the object more with the left eye, they manipulated it more with the right foot. Object novelty did not have an effect on the 'footedness' of a kakariki. This is as opposed to both the effect found in visual lateralisation and our hypotheses. Exploratory behaviour type did not have an effect in both the visual and motor lateralisation analyses. Thus, the population-level hemispheric specialisation explanation cannot necessarily be employed with kakariki.

Kakariki are high levels of lateralisation as individuals, but unlike many other parrot species studied to date (Harris, 1989; Snyder and Harris, 1997; Snyder and Bonner, 2001; Magat and Brown, 2009; Brown and Magat, 2011a,b), the direction of their lateralisation varies across their population. Brown and Magat (2011b) found that larger-bodied parrots displayed stronger laterality than smaller-bodied parrots. They argued that strong laterality was a fitness benefit for larger-bodied parrots, who frequently display complex bill-foot manipulations to extract well-embedded food items (e.g. nuts). Smaller-bodied parrots forage more by grazing or pecking (e.g. for blossoms or small seeds), and so do not require complex manipulatory abilities. As such, they suggested that there must be some unknown cost of laterality making it not worthwhile for small parrots.

Kakariki may be somewhere in between these two parrot groups, as they are both small-bodied and very lateralised at the individual level. This may reflect their very generalist diet, as kakariki eat both easy-to-pick blossoms and hard-to-extract nuts. So kakariki forage both by grazing/pecking and the more co-ordinated extractive foraging. Smith (1971) termed these two foraging techniques as 'tether-footed' and 'prehensile-footed' foraging. The

former involves clamping the food item between the holding foot and the supporting surface, thus requiring more vigilance behaviour than 'prehensile-footed' techniques, where the food item is brought up to the bill by the foot.

Alternatively, perhaps this lack of a population-level lateralisation in kakariki simply reflects the behavioural context in which the lateralisation was measured. The majority of literature has focussed on foraging behaviours, while we have looked at exploratory behaviours. Hemispheric specialisations for particular behavioural functions are common in birds, especially as non-conjugate eye movement enables birds to simultaneously scan the horizon for predators and the ground for food (reviewed in Rogers, 2000). This is especially relevant to consider together with our previous finding that relative to other bird species, parrots' eyes have an unusually large amplitude of independent movement, which is constantly changing (Demery et al., 2011). Further investigations are needed to distinguish between different potential lateralisations in parrots manipulating different types of objects in different contexts, including food items.

Lastly, it is interesting to consider the relationship between the visual field laterality and the foot motor laterality. They were found to be on contralateral rather than ipsilateral sides, as in Brown and Magat's (2009; 2011a) studies on Australian parrots. Both argued that this was consistent with other studies on more evolutionarily ancient animal taxa, such as fish and reptiles (Bisazza et al., 1998, 2001). This poses one of three possible explanations:

1. Kakariki have diverged from their ancestors both behaviourally and neurally in their pattern of lateralisation, possibly because of adapta-

tions to their particular ecological niche*;

2. Our new method of measuring eye preferences is inaccurate;
3. The method used to measure eye preferences by Brown and Magat (2009; 2011a) was inaccurate.

If point 1 were true, we have found a very exciting result and the possibility should certainly be explored further, including what sort of selection pressures may have resulted in the kakariki evolving in this way and what the possible distinctive underlying neural mechanisms may be. However, as the kakariki is an Australasian parrot, experiencing a very similar ecological niche to the many other Australasian psittacines already measured, this divergence is theoretically unlikely. Moreover, as this is such an unusual, yet stimulating, result, we must still take care with the potential problems outlined in points 2 and 3.

Both Brown and Magat's (2009; 2011a) method and our method are reasonable techniques for measuring eye preferences.. However, Brown and Magat's method makes the implicit supposition that if the object is held closer to one eye than the other, then the closer one is the fixating eye. Our previous research showed that there is a large binocular region in which both eyes can fixate (Demery et al., 2011). This means the bird can hold an object apparently in front of one eye while it is the other eye that is being used. The left foot does not need to bring the object to the right eye for it to be viewed by the right eye.

In order to come to a more definitive conclusion about points 2 and 3, we need to be able to draw a more direct comparison between the results of both

methods. Therefore, in a future study, we would ideally either: (a) apply our methods to the same species Brown and Magat measured; or (b) apply Brown and Magat's method to our birds from our video footage. Without further experimentation, in a direct comparison between the two studies the work presented here benefits from: frame-by-frame video analysis rather than live data entry; the use of a range of tests; and the use of a range of target objects rather than just food items. With this in mind, we would tentatively suggest that point 3 is the most likely.

4.4.4 Summary

These experiments have uncovered a complex pattern of how each eye, each limb and bill contribute to the sensorimotor exploration of different objects by kakariki. We would like to suggest that these sensorimotor adaptations are structured so that the kakariki can maximise the information gathered from the environment by exploratory learning. However, while our behavioural results are compelling, we can only *infer* from them about how, or even whether, the kakariki gathered and used information in their environment. We do not have any direct data on what the sensory signals were, or whether the kakariki were even exploring – they may have intended to perform some other executive action for some other biological function, such as foraging. There are clearly many other factors involved that have yet to be investigated. Indeed, it is not clear whether the technique we designed is even the correct one for the task, so this area is ripe for further research.

Nonetheless, our results have significant implications not only for how sensorimotor exploration is structured in other birds, but also for other animal groups, particularly in the field of cerebral lateralisation. While the bill

and the feet seem to be very important as sensorimotor apparatus for exploratory manipulation, vision still likely plays a significant role, especially during an exploratory approach. Further studies are needed to investigate more on how these senses interact and integrate to provide cross-modal information about objects.

Having investigated how vision and touch interact to support the exploratory approach and exploratory manipulation of an object in chapters 2, 3 and 4, we will continue to use the parrot model for studying exploration. However, from chapter 5 we will attempt to solve the problem of exploratory learning from a different angle, by investigating how the environment influences exploration.

Part II

Environmental Influences on Exploration

CHAPTER 5

The influence of environmental enrichment on exploration

Environmental enrichment is widely used as a means of improving captive animal welfare and it has been linked with improving cognitive problem-solving abilities (Newberry, 1995). We have exploited enrichment to investigate which kinds of information are important to kakariki when they explore dynamic environments. Parrots are found across the world in a variety of habitats. Among birds, they are distinctive for their intelligence, manipulatory abilities and strong exploratory tendencies. We measured exploratory behaviour in two captive groups of the social kakariki within their home cages and on an array of behavioural tests. Both groups received the same baseline level of environmental enrichment and the same feeding regime, but one group experienced a wider variety of materials in their cage (e.g. sawdust, perches in various diameters) and more problem-solving toys, provided on a rotation basis. We found that the more enriched group explored for significantly longer and displayed a greater diversity of behaviours than the less enriched group of kakariki. We also found that the enriched group were less neophobic and displayed greater exploratory complexity on the individual behavioural tests. This illustrates how, at least for kakariki, a few small changes to an animal's captive environment can have a substantial impact on their behaviour and potentially their performance in cognitive tests. It is not clear, however, whether these results could be generalised to the behaviour of kakariki living in the wild. We consider the results primarily within an information-processing perspective, but also discuss their implications for captive animal welfare.

5.1 Introduction

EXPLORATION is important for gathering information from the environment, whether it is to learn about novel objects, food, mates, predators or shelter (Archer and Birke, 1983; Power, 2000). How much variation, or how much potential information, there is in an animal's environment, influences the level of exploration required, as long as it impacts on the animal's evolutionary fitness in some way. For instance, an animal inhabiting an environment with a temperature range of -5–15ºC needs to explore and find drinkable water during particular parts of the year, unlike another animal living in 15–20ºC. There can be spatial or temporal variation (or both together), such as changes in food availability (e.g. Houston et al., 1980; Kacelnik and Krebs, 1985), or niche construction (Sterelny, 2007). In either case, the animal can overcome these changes by gaining information about them through exploration.

In an environment with relatively little variation, there is little new, potential information that can be gained, so there is not much need for exploratory learning. This allows for a large amount of information to be encoded in the animal's genes, but there is little selective pressure for flexible, adaptive behaviour (Gould, 1974; Kaelbling et al., 1998; Inglis et al., 2001). In more variable environments, factors are ever-changing, so an individual needs to be able to quickly adapt to a range of conditions; by gathering information through exploration (Roth et al., 2010; Rodewald et al., 2010; Sih, 2011; Chappell et al., 2012). The exploration level of a species is positively correlated with how variable its environment is (Bekoff, 1975; Seraglia et al., 2012; Greenberg and Mettke-Hofmann, 2001; Lefebvre et al., 2004; Pellis and Iwaniuk, 2004).

When faced with a variable environment, it is important for the animal to experience and learn about many different kinds of environmental information, so it can quickly solve any novel problems posed by the environment. These types of animals (e.g. great apes, corvids and psittacines, elephants, or cetaceans) are described as being cognitively flexible* *(e.g. Grasso and Basil, 2009; Tebbich et al., 2010; Auersperg et al., 2011).* Within a cognitively flexible species, genes initially provide all individuals with fundamentally the same exploration strategies and learning frameworks (Bekoff and Byers, 1998; Barsky, 2010). However, if there is no environmental information available for a particular individual to explore, their knowledge or understanding about the world cannot be extended (Povinelli and Dunphy-Lelii, 2001; Chappell and Sloman, 2007). So individuals with more experience of a wider range of environmental stimuli are likely to generalise information and learn flexibly about novel situations faster than inexperienced individuals (Chappell et al., 2012; Arriola-Rios et al., 2013). In other words, experienced individuals living in a more enriched environment are likely to be more innovative and better at problem-solving (Harlow et al., 1950; Mench, 1994; Greenberg, 2003; Mettke-Hofmann et al., 2006; Meehan and Mench, 2007; von Bayern et al., 2009; Roth et al., 2012).

How or even whether an animal will explore is determined not just by its experience, but also its intrinsic opposing motivations of neophilia* and neophobia* – the desires to either approach or avoid new items. Although neophilia clearly aids exploration, some animal groups, such as corvids, are noted as being both strongly neophobic and highly exploratory (e.g. Heinrich, 1995; Greenberg and Mettke-Hofmann, 2001). The zoological literature has reached a general consensus that efficient exploratory learning is further

influenced by another innate driver, uncertainty* reduction, i.e. a lack of stored information about the surrounding world (Hughes, 1997; Inglis, 2000; Koehler and James, 2009). Many animals seem to follow this principle – from fish, to birds, to mammals (Augustsson et al., 2005; Eliassen et al., 2007; Warburton and Hughes, 2011; Marsh and MacDonald, 2012). Even humans do so: children explore more when faced with ambiguous information (Schulz and Bonawitz, 2007; Beck et al., 2008; Bonawitz et al., 2012a); adults base their everyday decisions on an optimal trade-off between exploration and exploitation* (Daw et al., 2006; Cohen et al., 2007).

Exploration is not limited to the present. Individuals sometimes continually gather information without any immediate reward, simply for the possibility that it may be useful at some point in the future. This phenomenon, known as 'latent learning'*, has been extensively studied in rats (*Rattus norvegicus*) exploring mazes. They learn all the maze's paths without any incentive of a food reward and their exploratory activity increases when objects are moved within the maze; i.e. when uncertainty increases (e.g. Wilz and Bolton, 1971; Albert and Mah, 1972). Thus, while uncertainty is a strong driver, information-gathering is both energy and time consuming, so animals should only gather as much information as is needed (Grønhaug, 2006; Yoo, 2009). Dall and colleagues (Dall et al., 1999; Dall and Johnstone, 2002; Schmidt et al., 2009; Dall et al., 2012) illustrated how gathering information to reduce uncertainty is a luxury, but insuring against uncertainty by storing energy reserves is a necessity, at least when the animal is faced with starvation. Consequently, more insight is needed into how these different underlying motivations and environmental factors interact to impact on an individual's exploratory behaviour and the types of information experienced.

One way we could gain this insight is through environmental enrichment; i.e. chronically manipulating an animal's surroundings. To date, much of the literature into this has been from the perspective of improving a captive animal's welfare and cognitive well-being in zoos and in research laboratories. In this study, we will employ the following definition of environmental enrichment* as:

> "...an improvement in the [health or lifetime reproductive success] of captive animals resulting from modifications to their environment" (Newberry, 1995, p.230).

For instance, enhancing rodents' cage complexity, by adding a wider range of substrates (e.g. shredded paper or wooden blocks), or toys (e.g. foraging puzzles), increases exploration and natural activity patterns* in the short-term (Engellenner et al., 1982; Genaro and Schmidek, 2000; Gortz et al., 2008; Abou-Ismail et al., 2010), and increases cognitive performance and neophilia in the long-term (Gardner et al., 1975; Hennessy et al., 1977; Pisula and Stryjek, 2006; Huang et al., 2007; Brydges et al., 2011). Wood-Gush and colleagues (1990; 1991), through studies on pigs (*Sus scrofa*), highlighted the importance of providing 'inquisitive exploration' opportunities, where individuals act on and initiate changes in their environment, rather than just responding to a stimulus. Environmental enrichment has been shown to be important for humans' cognitive well-being too (e.g. Sumowski et al., 2010), but also for learning about different objects' affordances (e.g. Storli and Hagen, 2010). By extension, we would expect enrichment to be particularly important for other cognitively flexible species exploring variable natural environments, but this has rarely been considered, even within a controlled, captive

environment.

Applying an information-processing approach, in addition to the current animal welfare perspective, to environmental enrichment could be very fruitful. A few cognitive scientists have begun to systematically investigate the structure of exploration in different animals (e.g. rats, octopi and humans; Renner, 1988; Kuba et al., 2006a; Schulz et al., 2008). However, none of them have utilised environmental enrichment as a means of investigating what kinds of environmental information are important to different species. For instance, it is important for a honey-bee (*Apis mellifera*) to explore in order to learn which flowers are currently producing nectar where, but it is not clear what kind of environmental cues (e.g. olfactory or visual) they focus upon (Srinivasan and Gregory, 1992; Menzel and Giurfa, 2006; Avargues-Weber et al., 2011; Arenas and Farina, 2012). Environmental enrichment increases an animal's exposure to new materials and more causal events, and consequently likely impacts on their cognitive performance and learning of important environmental information (Forster, 1995).

The environmental influence on exploration is therefore approachable through enrichment; an idea we applied to parrots in this study. After introducing different complex toys and various materials, we measured the resultant possible effects on parrots' exploratory behaviour. We wanted to consider what parts of the environment may be important to psittacines when gathering information and how their exploratory behaviour may vary with the properties of the object they are investigating. It is important to note though that by observing exploratory behaviour, we cannot directly conclude what types of information an animal is gathering. Depending on what form of

enrichment we provide, we can only ever infer what information we are *potentially* providing the animal with.

Parrots have strong exploratory tendencies and neophilia that lasts into adulthood, even when it is not motivated by food (Pepperberg and Brezinsky, 1991; Luescher, 2006; Demery et al., 2011). They often display innovative, flexible behaviour for solving diverse environmental problems (e.g. Huber and Gajdon, 2006). This is aided by dextrous manipulatory abilities with zygodactyl* feet and a hooked bill (Smith, 1975). Moreover, they live long lives in a variety of (frequently variable) habitats and many psittacine species are food generalists (Collar, 1997; Rowley, 1997). Mettke-Hofmann and colleagues (1995; 2000; 2002; 2005) found that psittacine exploration is sensitive to a range of environmental factors, including: courtship and breeding periods; diet type (e.g. seasonal/cryptic food items); habitat complexity (e.g. forest edges); migratory behaviour (resident/nomad); and predation risk (e.g. on island/mainland).

Captive parrots, without appropriate enrichment, are particularly susceptible to developing abnormal* and stereotypical behaviour*, such as feather picking, or repetitive locomotory routes like 'corner-flipping' (van Hoek and ten Cate, 1998; Evans, 2001; Garner et al., 2003, 2006; Lumeij and Hommers, 2008). Enrichment through greater foraging opportunities (e.g. nuts in a hanging basket), or physical complexity (e.g. ropes to climb on), has been shown to modify neophobia and motivation for environmental interaction (Meehan and Mench, 2002; Meehan et al., 2002; Lumeij and Hommers, 2008; Webb et al., 2010). A few researchers have started to investigate which particular properties of objects (e.g. toys) parrots find stimulating. Orange-winged

parrots (*Amazona amazonica*), for instance, have a preference for small, soft, yellow cubes over a range of other variations, and exhibit sex-specific preferences for rope length, diameter and colour (Kim et al., 2009; Webb et al., 2010). This may reflect the appearance of food items found in the wild (Janson, 1983), or sex differences in allopreening (Spoon et al., 2004). However, none have yet investigated the effect of enrichment on psittacine exploration, particularly from an information-processing perspective.

Consequently, the aim of our study was to investigate how environmental enrichment may influence exploration in captive parrots under different environmental contexts. Our chosen study species was the New Zealand red-fronted parakeet or kakariki (*Cyanoramphus novaezelandiae*), as they are especially social, neophilic and active compared to other psittacines (Pepperberg and Funk, 2005), which makes them an ideal species for studying exploration. They show high dexterity in manipulating objects, and they use the same method of extracting seeds as found in nearly all Psittaciformes (Collar, 1997). Kakariki can be found at all strata of temperate rainforests, but they are also resident to scrub and grassland habitats. They mature at approximately 9 months and live for 5–10 years. They have a highly generalist diet, largely consisting of seeds, fruit, leaves, buds, flowers, shoots, and nectar, but also insects, animal remains, tiny stones, as well as seaweed and mussels in coastal areas (Greene, 1988, 1998; Kearvell et al., 2002; Funk and Matteson, 2004).

We housed two groups of kakariki in different enrichment conditions, then measured their exploration in two environmental contexts: within their home cage and across various behavioural tests. Both groups received the

same baseline level of environmental enrichment and the same feeding regime, but one group experienced a wider variety of materials in their cage and more problem-solving toys. The enriched enclosure would provide more potentially new information, so the enriched kakariki would likely be motivated to explore within both environmental contexts more than the unenriched kakariki, which would reach a ceiling amount of information (Wood-Gush et al., 1990; Renner, 1990). Therefore, we predict that relative to the unenriched group, the enriched group will spend a greater proportion of time exploring and perform a greater variety of exploratory behaviours. On the other hand, Meehan and Mench (2002) found unenriched orange-winged parrots explored more than their enriched counterparts, perhaps because enriched individuals have more experience, so they do not need to explore novel objects as much as unenriched individuals. Thus, the alternative prediction is that the enriched kakariki would explore less than the unenriched kakariki.

Specifically within the home cage context, we were interested in what aspect of the environment enriched and unenriched individuals focussed their exploration upon. One difference in enrichment that we manipulated between each group was the complexity of toys present. More complex items are likely to provide richer information than simpler items (Meehan et al., 2002; Mettke-Hofmann et al., 2006). Thus, here we hypothesise that the enriched group will spend a greater proportion of their exploratory time interacting with toys as opposed to other home cage features (e.g. mesh, perches, water bowl). Conversely, we suggest the unenriched group will display no significant preference for toys over the other cage features.

Lastly, within the behavioural testing context, we were interested in the relative complexity of exploratory behaviours performed on the same novel test objects by the enriched and unenriched kakariki. The enriched kakariki would have more experience of a greater range of objects and affordances from their home cage, so they would also have greater experience of using a greater diversity of behaviours to gather information (Sol et al., 2005; von Bayern et al., 2009). Hence we hypothesise that the enriched group will spend a greater proportion of exploration time performing complex exploratory behaviours than the unenriched group. We further wanted to investigate how neophobia may affect unenriched birds' exploratory approach towards a novel object under testing conditions (e.g. see Greenberg, 2003; Pisula and Stryjek, 2006). These birds were not as exposed to as great a range of novel objects as the enriched birds, so they were not as accustomed to objects posing little threat. Consequently, we postulate the enriched group will show a significantly shorter latency to the first exploration bout than the unenriched group, but this effect will be lessened when the object is familiar, rather than novel.

5.2 Methods

5.2.1 Subjects

The subjects were 14[1] kakariki (*Cyanoramphus novaezelandiae*; 7 females; 7 males). They were parent-raised and were sourced from four different breeders in the United Kingdom, so they were probably hybrids with the yellow-fronted parakeet (*C. auriceps*; Boon et al., 2001). They were delivered from the

[1]Note this number differs from the 20 subjects studied in chapter 4, as in this chapter we only studied the adult kakariki present before any breeding occurred (from April 2010 onwards), to avoid possible effects an increased number on birds in some cages.

breeders when they were 3 months of age, then quarantined for 28 days (all hatched April – May 2008).

5.2.2 Housing

All of the kakariki were housed indoors according to guidelines set out in Hawkins et al. (2001) and Kalmar et al. (2007; 2010). They were kept in a temperature-controlled environment (23 ± 5ºC) on a 12:12 light cycle (dark from 8 pm to 8 am daily; UV daylight light bulbs with a high flicker frequency). The kakariki were housed in pairs in adjoining aluminium cages, each sized 1.83 x 1.22 x 1.22 m. They were cleaned out weekly and fed daily at 11 am on a diet of fresh fruit and vegetables with a parrot seed mix (Parrot Mix Royale, Copdock Mill, Ipswich, UK). Wood chips (Lillico Biotechnology, Surrey, UK), water baths and a range of toys and ropes were provided.

The kakariki were allocated to either the 'unenriched' housing condition or the 'enriched' housing condition (4 unenriched pairs and 3 enriched pairs). Each group was housed in separate rooms. We call the less enriched or control condition 'unenriched', although the birds housed in this condition were not actively deprived of any of the recommended requirements (Hawkins et al., 2001; Kalmar et al., 2007, 2010). The 'unenriched' birds were enriched to some degree, but they were not exposed to as many different objects and materials as the 'enriched' group.

The enriched group was exposed to a wider range of the perch types, materials and substrates (Table 5.1). The enriched group was also presented with 'complex toys', which enabled more complex cognitive behaviours. These toys were designed to stimulate problem-solving abilities (e.g. remove

Table 5.1 – Details of the differences between the 'enriched' and 'unenriched' housing conditions. The key difference is the amount of exposure to different perches, materials and substrates, and in the complexity of the toys. See Figure 5.2.1 and Appendix D for more details on the different toys.

Group	Home Cage Features
Unenriched	◇ 3 natural wooden perches of similar lengths and diameters (approximately 60 cm long, 5 cm in diameter)
	◇ 3 hanging ropes (60 cm long, 5 cm in diameter)
	◇ 3 simple toys, where position in cage rotated weekly (e.g. affording basic climbing or manipulation opportunities)
Enriched	◇ 3 natural stick perches of varying lengths and diameters
	◇ 3 ropes of different thicknesses (e.g. string versus thick hemp) twisted in different ways (e.g. knots, loops etc.)
	◇ Wood chips containing different substances (e.g. more grit, sand, mud, seed etc.)
	◇ Novel materials, including rubber, sponge, ceramics
	◇ 3 complex toys rotated between cages weekly (e.g. stimulating problem-solving abilities or causal understanding)

nut from puzzle box), or causal understanding* (e.g. connected cogs turning when lever pulled down), and exposed the birds to a wider range of materials (Figure 5.2.1 or for more details Appendix D). The complex toys were rotated between each enriched cage on a weekly basis. In contrast, the cages of the unenriched group were each provided with the same 'simple toys' that were not rotated between cages. These simple toys afforded simpler behaviours than the complex toys, such as basic climbing or manipulation opportunities (e.g. on a rope swing or chewing fibres on a mop-head). While these toys were not rotated in the unenriched cages, the position of the toys (the side of the cage and the height at which they were attached) was altered week-to-week.

Figure 5.2.1 – Toys in the enriched and unenriched conditions (Northern Parrots, Ramsbottom, UK). The toys above the line were the simple toys in the unenriched condition, which particularly enabled behaviours like climbing or simple manipulations (e.g. chewing). These toys stayed in the same cages, but their position within the cage changed weekly. The toys below the line were the complex toys in the enriched condition, which were rotated on a weekly basis between cages. They were designed to encourage problem-solving and causal understanding abilities. See Appendix D for more details on the individual toys.

5.2.3 Home cages analysis

A motorised camera (Logitech Quickcam Sphere AF) was set up in each room to continuously record the kakariki in their home cages from March 2009 to April 2010 onto an external hard-drive (Western Digital 500 GB MyBook; or Buffalo Drivestation 1TB USB 2.0 External Hard Drive), using the software Debut Video Capture Pro (v. 1.64; NCH Software, Canberra) installed on a small laptop (ASUS Eee PC 904HD, Microsoft Windows XP; or Samsung N130 notebook, Microsoft Windows 7 Starter). Each video was recorded in 30-minute blocks in H264-MPEG-4 avc1 format (25 fps; 480x270 resolution).

The videos were analysed by performing 5-minute focal watches of each individual in each cage, for each fortnight of video recording (total 364 focal watches, or approximately 30 hours of analysed video). The time of day and the date for each 5-minute video sample (per bird per 14 days) was selected randomly, but Fridays (when the birds were cleaned out), as well as the first and last hour of each day, and 10.30 am – 12.00 pm (over the feeding period) were excluded. If the selected 5-minute sample contained periods when the bird was out-of-sight of the camera, or a human was present in the room, a different 5-minute sample was pseudo-randomly selected on that date.

During each focal watch, the focal bird's behaviour was recorded using the ethogram outlined in Appendix C and JWatcher Video version 1.0 (Blumstein et al., 2007). We will refer to the object that the bird happens to be interacting with (i.e. the 'target object' as referred to in other chapters) as the 'object of interest'. Briefly, the ethogram consisted of five exploratory behaviour categories and five non-exploratory behaviour categories (e.g. maintenance or social behaviours). The exploratory behaviour categories were divided into 31 sub-categories, while the non-exploratory behaviour categories were divided into 20 sub-categories. The five main exploratory behaviour categories were:

- visual inspection (e.g. follow, search);
- grasping (transitory e.g. tap; or prolonged e.g. carry);
- actions (e.g. push, pull);
- modifying objects (e.g. bend, pry);
- relating objects (e.g. insert, hook).

With each behaviour category, the following was also recorded: whether the

behaviour was targeted at a toy (e.g. rotating cog toy) or a non-toy cage feature (e.g. splashing in water bowl); whether the behaviour was targeted at the focal individual itself (e.g. preening wing), or at a conspecific (e.g. courtship with mate); and whether a conspecific was within grasping distance (within 5 cm) of the focal individual or the target object. This allowed analysis for any consistent patterns of behaviour, but also produced an overall measure for each trial as follows:

- proportion of time spent exploring;
- number of different exploratory behaviours ('behavioural diversity');
- and proportion of time spent with different cage features (i.e. toys versus non-toy features like water bowl, perch, mesh etc.).

It is important to note that, although the toys in the enriched enclosures were more complex and the enriched birds were exposed to a wider a range of materials than the unenriched birds, a pilot study confirmed that theoretically *all* of the behaviours described in the ethogram could be performed by both groups of kakariki.

5.2.4 Behavioural tests analysis

Test trial sampling

In addition to the analysis of home cage exploratory behaviour, exploratory behaviour performed under behavioural test conditions was also analysed. None of the work conducted for this project required a Home Office Licence and all the techniques used were non-invasive, following the guidelines set out by the UK Animals (Scientific Procedures) Act, 1986. There were a series of behavioural tests conducted between March 2009 and April 2010. Primar-

ily conducted for a separate study (chapter 6), they investigated how different object properties influence the pattern of exploration for a separate study. However, they also proved ideal for this environmental enrichment analysis, so here we sampled a selection of their test trials. The analysed dataset was based on the live recordings from the selected trials. While the general protocol was consistent across tests, the test object, and whether it was familiar or novel, varied between tests (Figure 5.2.2). 'Familiar' was defined as the subject having experienced the target object at least once in a previous trial and 'novel' as when they had not.

Note that while the trials were selected pseudo-randomly for analysis, the analysed data for each trial accounted for the trial's entire test trial time (25 minutes). Specifically, four trials were selected for each subject, one from each three-month period. The date selected for each video for each individual was pseudo-randomised, with the constraint that across individuals there were an equal number of trials occurring in the morning and afternoon.

This method of date selection determined that the type of behavioural test being performed and whether the target object was familiar or novel at that sampled date was pseudo-randomised. Despite this, there was an approximately equal number of trials (from all individuals) across the different behavioural tests and an equal number of trials with a novel object and a familiar object, so there was no overall bias in the dataset. Within each enrichment group, there were approximately an equal number of analysed trials with familiar objects and novel objects.

Figure 5.2.2 – Illustrations of all the test objects.

General test protocol

The test object was set up on a table within a custom-made test cage (67 x 58 x 60 cm) before the subject entered the test room. The experimenter sat on the other side of a solid screen in front of the apparatus to avoid visual cueing. The subjects' behaviour was monitored remotely and recorded via two video cameras (Sanyo Xacti VPC-CG10, recorded using MPEG-1/2 codec, 720x576 resolution, 30 fps) positioned perpendicular to the test cage, above and to the side of it. There was a habituation period of five minutes, then the trial lasted 25 minutes. Each kakariki never entered into more than one trial each day.

The time of day that each individual was moved to the test room was

pseudo-randomised between 0900 and 1700 between days. The kakariki were trained to individually enter and exit a portable transport cage (81 x 42 x 61 cm), by means of a food reward (strawberry). To ensure that the birds' attention was drawn to the link between entering/exiting the cage and the reward a clicking sound (produced by a standard dog training device) was employed to seize their attention. When, infrequently, a net was required to catch the bird, an extra five minutes of habituation was allowed in the test room.

All of the ensuing behaviours were recorded live via remote monitoring using JWatcher, according to the same ethogram as used in subsection 5.2.3. For this behavioural tests analysis, each exploratory behaviour category was assigned one of three levels of complexity, according to how cognitively and physically difficult it was for the bird to perform the behaviour. Complexity was greater when a behavioural category required multiple appendages, and/or became focussed on multiple objects or object parts. For instance, 'simple' behaviours included categories like tapping or holding. Whereas 'intermediate' behaviours included rotating or translating an object, and 'complex' behaviours largely consisted of behaviours that modified or related object parts together (e.g. scraping or extracting). Note that despite the difference in exposure to toy complexity and materials in the home cage environment, a pilot survey confirmed that both groups of kakariki could theoretically have performed all levels of behavioural complexity with the actions afforded by items within their home cages prior to testing.

For each behavioural test trial, the same exploratory variables were analysed as for the home cage exploration. Additionally, the proportion of exploration time spent performing behaviours of different levels of complex-

ities (simple, intermediate, complex) and the latency to the first exploration bout (first touch made to object of interest) was included in this behavioural test analysis. Two consecutive bouts were defined as separate bouts when they were separated by 10 seconds or more.

5.2.5 Statistical methods

For both the home cages and the behavioural test data, the proportion of time spent exploring and the behavioural diversity was analysed using a repeated measures General Linear Model. These measures were calculated from means of each individual across test types and sampled videos. Note for the effects of explored cage features (in home cage analysis), exploratory behaviour complexity and object novelty (in behavioural test analysis), the proportions were adjusted for each group accordingly (see respective results section below for clarification). The assumptions of parametric methods (normality of error, homogeneity of variance and linearity) were confirmed from plots of coefficients versus fitted values. Where proportional data measures were used, the data was arcsine-squareroot transformed. All analyses were performed using Minitab® Statistical Software version 15.1.30. The probability level accepted for significance was $p < .05$.

In all of the models, where significant effects were found, a series of post-hoc pair-wise Tukey tests were performed to find the source and direction of the significance. The exception to this was in the behavioural tests' exploratory complexity analysis, where a series of post-hoc pair-wise paired and unpaired *t*-tests were performed (unpaired for between housing groups and paired for within groups).

In all of the models, the following factors were also included to check whether they had an effect on the general exploration measures: sex, age, origin (i.e. breeder), and cage position. Within the home cage analysis, the proportion of the time sampled where a conspecific was within grasping distance of the focal individual or the object of interest was incorporated into the model. Within the behavioural test analysis, the number of trials where the bird was caught with a net was incorporated into the model. As the general key measures were means for each of the 14 kakariki across focal watches or sampled videos, a series of unpaired *t*-tests were performed on each individual, to check whether the time, date or the test type of the sampled video had an effect on the proportion of time spent exploring.

5.3 Results

The home cage or behavioural test exploration measures were not significantly affected by the time or date of the video. Similarly, in the GLMs, neither were they significantly affected by the kakariki's sex, age, breeder or cage position. Within the home cage environment there was no significant effect of a conspecific being within grasping distance of the focal individual or the target object. Likewise for the behavioural tests measures, there was no significant effect of the bird having been caught with a net or not prior to testing.

5.3.1 Home cages

Exploration and behavioural diversity

In their home cage, the enriched group explored for a significantly greater proportion of the sampled time (GLM: $F_{1,7} = 45.95$; $p < .001$; Figure 5.3.1a) and displayed a significantly greater mean number of different exploratory

Table 5.2 – A summary table outlining the three GLM models for effects of housing enrichment on: the proportion of the sampled time kakariki spent exploring within the home cage environment; their behavioural diversity (number of different exploratory behaviour); and the proportion of the sampled time spent exploring different cage features. This proportional data was arcsine-squareroot transformed. Sex, cage position (close to door, middle, furthest from door) and breeder (6 breeder IDs) were included in both models as fixed factors, while age and the proportion of time sampled where a conspecific was within grasping distance of the focal individual or the object of interest were included as covariates. The latter was also arcsine-squareroot transformed. Enrichment (enriched or unenriched kakariki group) was a fixed factor in the models. In the last model, cage feature (toy or non-toy feature) was also a fixed factor.

	Factor	**d.f.**	***F***	***p***
% time sampled spent exploring$^{\diamondsuit}$	**Enrichment**	**1**	**45.95**	**< .001**
	Sex	1	3.24	0.115
	Cage position	**2**	**6.81**	**0.023**
	Breeder	5	0.74	0.618
	Age	1	0.16	0.699
	% time near conspecific	1	0.26	0.625
no. different exploratory behaviours$^{\diamondsuit}$	**Enrichment**	**1**	**8.40**	**0.023**
	Sex	1	0.77	0.409
	Cage position	2	0.40	0.682
	Breeder	5	0.27	0.916
	Age	1	0.03	0.878
	% time near conspecific	1	0.59	0.466
% time sampled spent exploring different cage features$^{\sun}$	Enrichment	1	0.00	1.000
	Cage feature	**1**	**46.13**	**< .001**
	Enrichment × Cage feature	**1**	**33.91**	**< .001**
	Sex	1	0.03	0.982
	Cage position	2	0.07	0.779
	Breeder	5	0.01	0.993
	Age	1	0.00	1.000
	% time near conspecific	1	0.68	0.371

Significant variables are indicated in bold. $^{\diamondsuit}n = 14$ $^{\sun}n = 28$

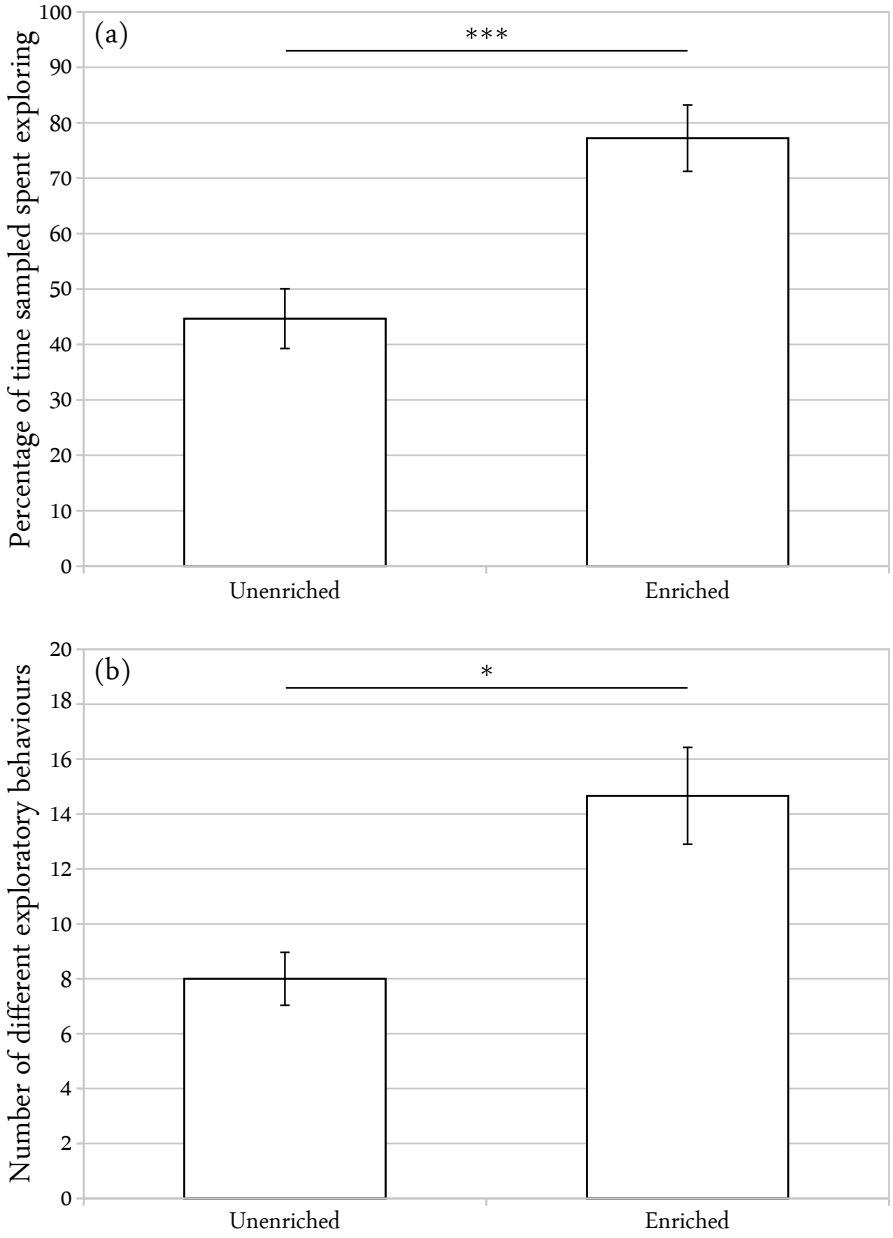


Figure 5.3.1 – A bar chart illustrating the exploration displayed by enriched and unenriched kakariki (*Cyanoramphus novaezelandiae*) in their home cages using two general measures: **(a)** percentage of 5-minute focal watch spent exploring; and **(b)** behavioural diversity (number of different exploratory behaviours). The key difference between the enrichment groups was in the amount of exposure in their home cage to different perches, materials, substrates and toys (Table 5.1 and Figure 5.2.1). There were 14 kakariki altogether and this data was based on each bird's mean across 26 focal watches from March 2009 to April 2010. The error bars reflect the standard-error-of-the-mean. The lines over the each pair of bars indicates a significant difference between that pair at either $p < .05$ (*), $p < .01$ (**) or $p < .01$ (***; Tukey Test).

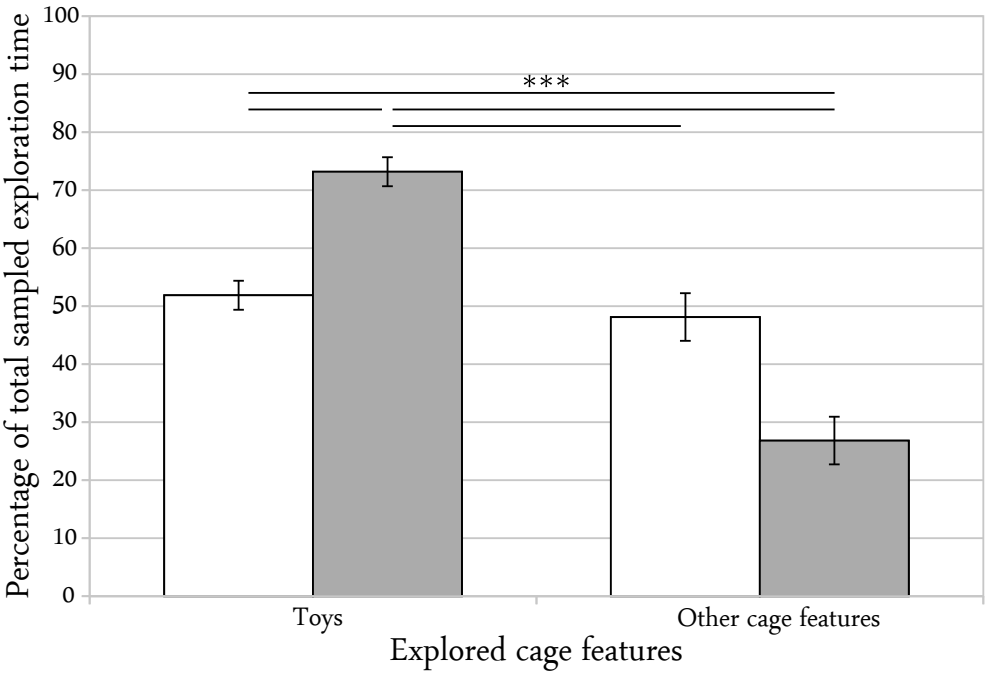


Figure 5.3.2 – A bar chart illustrating the percentage of (total sampled) exploration time enriched (in grey) and unenriched (in white) kakariki spent exploring toys and other cage features in their home environment. 'Other cage features' refers to any feature in the cage that was not one of the toys shown in Figure 5.2.1, such as cage mesh, water bowls or perches. This figure caption corresponds to Figure 5.3.1.

behaviours within a focal period (GLM: $F_{1,7} = 8.40$; $p < .05$; Figure 5.3.1b; Table 5.2) than the unenriched group.

Different home cage features

For the the proportion of the total sampled exploration time, a significant effect of explored cage part (GLM: $F_{1,19} = 46.13$; $p < .001$) and a significant interaction of explored cage part and enrichment group was found (GLM: $F_{1,19} = 33.91$; $p < .001$; Figure 5.3.2; Table 5.2). A series of post-hoc pair-wise Tukey tests were then conducted. The enriched group spent a greater proportion of the total sampled exploration time exploring the toys in their home cage as opposed to the other cage features (Tukey: $p < .001$). In contrast, the unen-

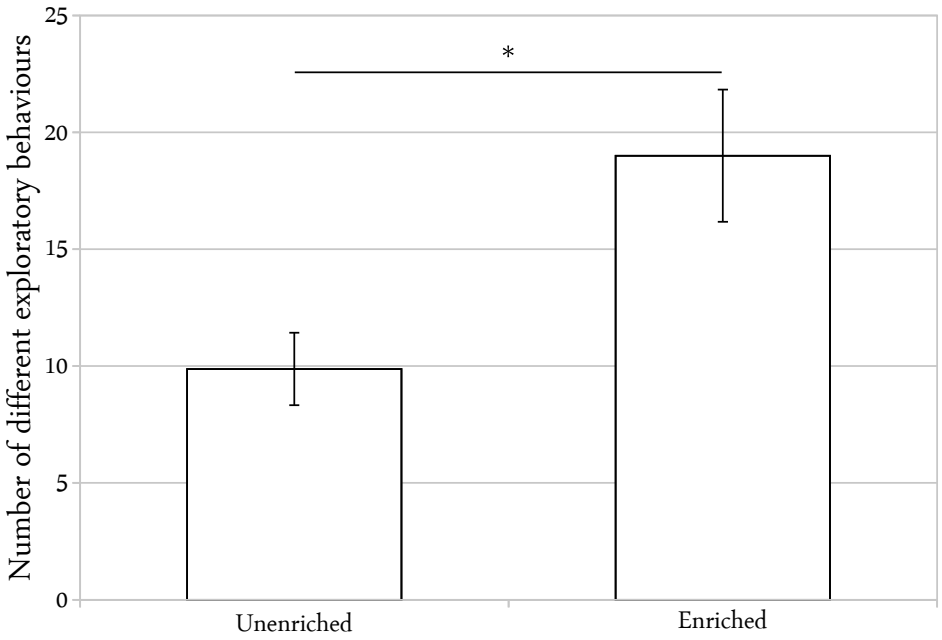


Figure 5.3.3 – A bar chart illustrating the exploratory behaviour diversity displayed by enriched and unenriched kakariki (*C. novaezelandiae*) under test conditions. The key difference between the enrichment groups was in the amount of exposure in their home cage to different perches, materials, substrates and toys (Table 5.1 and Figure 5.2.1). There were 14 kakariki altogether and this data was based on each bird's mean from four videos of various behavioural tests conducted between March 2009 and April 2010. The tests investigated different aspects of exploration and so each involved slightly different protocol and objects of interest (section 6.2 on page 171). The error bars reflect the standard-error-of-the-mean. The lines over the pair of bars indicates a significant difference between that pair at either $p < .05$ (*), $p < .01$ (**) or $p < .01$ (***; Tukey Test).

riched group showed no significant difference between the proportion of the exploration time spent on the toys versus the other cage features (Tukey: $p > .05$).

5.3.2 Behavioural tests

Exploration and behavioural diversity

Across the behavioural tests, the enriched group displayed a significantly greater mean number of different exploratory behaviours within a trial than

Table 5.3 – A summary table outlining the four GLM models for effects of housing enrichment on: the proportion of the trial time spent the kakariki spent exploring under behaviour test conditions; their behavioural diversity (number of different exploratory behaviour); the proportion of exploration time performing different complexity levels of exploratory behaviour; and the latency to the first exploration bout (in seconds) for the kakariki exploring novel and familiar objects. The proportional time data was arcsine-squareroot transformed. Sex, cage position (close to door, middle, furthest from door) and breeder (6 breeder IDs) were included in both models as fixed factors, while age and the number of trials where the kakariki was caught with a net were included as covariates. Enrichment (enriched or unenriched kakariki group) was a fixed factor in the models. In the third model, exploratory behaviour complexity (easy, intermediate and difficult), while in the last model, object novelty (novel or familiar) were also fixed factors.

	Factor	**d.f.**	***F***	***p***
% exploration time$^{\diamondsuit}$	Enrichment	1	0.05	0.853
	Sex	1	0.39	0.551
	Cage position	2	0.60	0.576
	Breeder	5	0.63	0.683
	Age	1	0.68	0.437
	No. trials net	1	1.04	0.342
no. different exploratory behaviours$^{\diamondsuit}$	**Enrichment**	**1**	**5.69**	**0.049**
	Sex	1	0.01	0.917
	Cage position	2	0.92	0.443
	Breeder	5	2.04	0.189
	Age	1	0.45	0.526
	No. trials net	1	0.41	0.544
% exploration time in different exploratory complexities$^{\varsigma}$	Enrichment	1	0.00	0.989
	Complexity	2	0.09	0.912
	Enrichment × Complexity	**2**	**6.97**	**0.003**
	Sex	1	0.02	0.896
	Cage position	2	0.01	0.989
	Breeder	5	0.00	1.000
	Age	1	0.00	0.971
	No. trials net	1	0.03	0.870
latency to first exploration bout*	**Enrichment**	**1**	**58.83**	**< .001**
	Object novelty	**1**	**24.17**	**< .001**
	Enrichment × Object novelty	**1**	**35.70**	**< .001**
	Sex	1	0.01	0.922
	Cage position	**2**	**4.16**	**0.032**
	Breeder	5	0.00	1.000
	Age	1	0.12	0.731
	No. trials net	1	0.51	0.482

Significant variables are indicated in bold. $^{\diamondsuit}n = 14$ $^{\varsigma}n = 42$ $^{\star}n = 28$

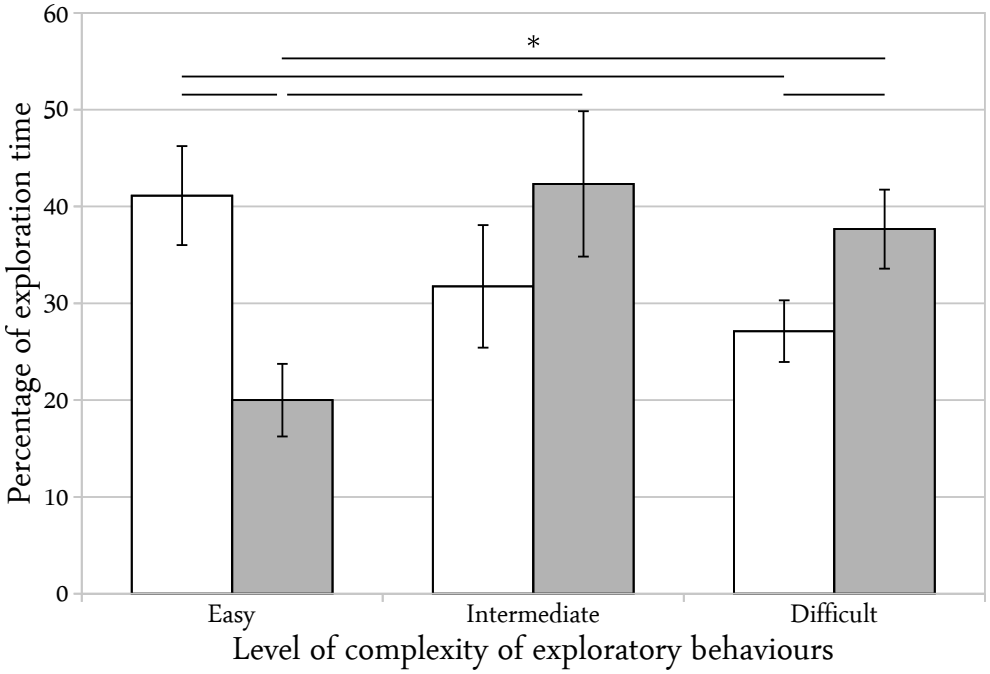


Figure 5.3.4 – A bar chart illustrating the percentage of exploration time enriched (in grey) and unenriched (in white) kakariki spent performing three complexity levels of exploratory behaviours under test conditions. Each exploratory behaviour category was allocated one of three complexity levels according to how cognitively and physically difficult it was for the bird to perform the behaviour (Appendix C). This figure caption corresponds to Figure 5.3.3, except that the post-hoc tests were carried out using a series of paired and unpaired *t*-tests.

the unenriched group (GLM: $F_{1,7} = 5.69$; $p < .05$; Figure 5.3.3; Table 5.3). However, there was no significant difference in the mean proportion of the trial time spent exploring between the enriched group and the unenriched group (GLM: $F_{1,7} = 0.04$; $p > .05$).

Complexity of exploratory behaviours

Across the behavioural tests, there was a significant difference between the enriched group and the unenriched group for the mean proportion of the trial exploration time spent performing different levels of behavioural complexity (GLM: $F_{2,31} = 6.97$; $p < .01$; Table 5.3). A series of post-hoc pair-wise

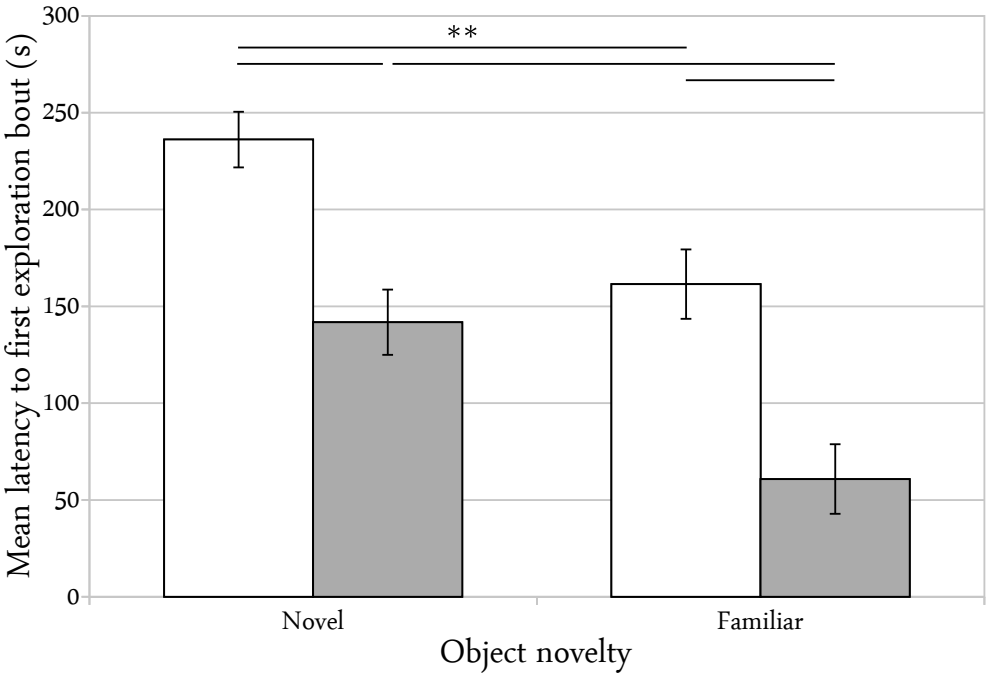


Figure 5.3.5 – A bar chart illustrating the mean latency to the first exploration bout (in seconds) for enriched (in grey) and unenriched (in white) kakariki exploring novel and familiar objects under test conditions. The bout was defined as having started from the bird's first touch of the object of interest. A 'familiar' object was defined as the bird having experienced the object at least once in a previous trial and 'novel' was when they had not. This figure caption corresponds to Figure 5.3.3.

comparisons using unpaired *t*-tests were run and Figure 5.3.4 illustrates all of the differences. Most notably, the enriched group spent a significantly greater proportion of the exploration time performing complex behaviours than the unenriched group (unpaired *t*-test: t_{10} = -3.24; $p < .01$). In contrast, the unenriched group spent a significantly greater proportion of the exploration time performing simple behaviours than the enriched group (unpaired *t*-test: t_9 = 2.76; $p < .05$). There was no significant difference between the two enrichment groups for the proportion of exploration time spent on the intermediate behaviours (unpaired *t*-test: t_6 = 0.52; $p > .05$).

Latency to first exploration bout and object novelty

If the object within a trial was novel, then the mean latency to the first exploration bout was greater than if the object was familiar (GLM: $F_{1,19} = 24.17$; $p < .001$; Table 5.3). Overall, the unenriched group had a significantly longer mean latency to their first exploration bout within a trial than the enriched group (GLM: $F_{1,7} = 58.83$; $p < .001$). There was a significant interaction between this effect of enrichment group and the effect of object novelty on latency (GLM: $F_{1,19} = 35.70$; $p < .001$; Figure 5.3.5). Therefore, if an object was novel, then the latency to the first exploration bout was even greater in the unenriched group than in the enriched group (Tukey: $p < .01$).

5.4 Discussion

Our results show that, at least for psittacines, small changes to the captive home cage environment can result in substantial changes in behaviour. This affects not only their activity and exploration in the home cage, but also their behaviour and potentially their performance in behavioural tests. To our knowledge, this is the first time that an enrichment effect on behaviour has been extended beyond the captive enclosure environment. In other words, the significant difference we found in exploration between the enriched and unenriched kakariki was not specific to the objects added to their cages, but was also found with novel items in a test room environment, separate to the home cage environment. We have just begun to uncover how the environment influences the pattern of exploration..

5.4.1 Exploration and behavioural diversity

As hypothesised, the group of kakariki housed in the enriched condition spent more time exploring in their home cage than the group of kakariki housed in the unenriched condition, although under test conditions there was no difference in the proportion of time spent exploring between the groups. The enriched group also displayed a greater diversity of exploratory behaviours towards the object of interest in both their home cage and under test conditions than the unenriched group. The main difference in housing was that the enriched group were exposed to a wider range of materials than the unenriched group, such as different ropes or artificial materials like rubber. The enriched group also experienced more complex toys (e.g. foraging puzzles or rotating cogs), which were rotated on a weekly basis. Conversely, the unenriched group received the same simple toys week-to-week. These toys did not have as wide a range of properties as those in the enriched cages.

The objects available in the unenriched condition did allow for all the behaviours described in the ethogram (Appendix C), as did the objects in the enriched condition. Nonetheless, the unenriched group did not display as great a diversity of behaviours as the enriched group in their home cage. This may be because the enriched kakariki were more *motivated* to explore (Hughes and Duncan, 1988; de Lorge and Bolles, 1961). Potentially, there was more new information available to gather in the enriched enclosure, so the kakariki here were motivated to try out a wider range of behaviours on the novel items. Conversely, the unenriched kakariki may have reached a ceiling; they had already gathered as much information as they could and as they needed about their environment (Jennings et al., 1979; Cohen et al., 2007; Pullen et al., 2012).

It is not clear whether the unenriched or enriched kakariki within their enclosure managed to display exploratory levels qualitatively similar to those exhibited by parrots in the wild, as the focus of field studies has been on parrot foraging (rather than exploratory) activity (e.g. Smith, 1975; Greene, 1998; Luescher, 2006; Rozek et al., 2010) – but these are not mutually exclusive. For example, a closely related parrot to the kakariki, the crimson rosella (*Platycercus elegans*) has described to spend 44–55% of their day foraging or locomoting around the canopy (Magrath and Lill, 1983). We suggest that each of these behaviours may to some extent be exploratory, whether the birds are gathering information about potential food items, areas of shelter in the canopy, or about potential mates.

Even under test conditions, the unenriched individuals were not as behaviourally diverse as the enriched individuals in their exploration. This suggests the unenriched individuals did not have as much information about the world as the enriched individuals. The lack of behavioural diversity implies the unenriched individuals' object exploration was more repetitive and perserverative* than enriched individuals', who were more varied in their exploration patterns. Exploratory variation (or 'flexibility') may be an indicator of progressively more sophisticated exploration strategies for more efficient learning (Arriola-Rios et al., 2013). Experiments on human children's exploration strategies reveals that during their cognitive development there is a progression from trial-and-error, perserverative behaviour to more sophisticated, targeted exploration strategies (e.g. Piaget, 1974; Gibson, 1988; Ruff et al., 1992; Power, 2000; Rochat, 2001; Pellegrini and Smith, 2004; Schulz et al., 2007).

Meehan and Mench (2002) have shown the opposite effect with orange-winged parrots, where unenriched individuals explored more than enriched individuals when faced with a novel item. Unenriched individuals also seemed to seek out more stimulation, such as from human handlers or food pieces in their water bowl. Perhaps a starvation of information actually motivates an individual to seek it out more (Sahakian et al., 1977; Vestergaard, 1982; Houpt et al., 2001). However, the different results found in Meehan and Mench (2002) may just be due to a species difference, or how our birds were not as unenriched as the birds in this study, which were actively deprived of quite basic stimulation in their cage environment (Hughes, 1997; van Hoek and ten Cate, 1998). Further investigation is needed to determine whether unenriched birds do lack information that enriched birds possess. Other studies have illustrated that enriched individuals do have more experience of particular object properties and adapt their behaviour accordingly (Renner, 1988; Varty et al., 2000; Fox and Millam, 2004; Mettke-Hofmann et al., 2006; Haun et al., 2010; Roth et al., 2012). Thus, there seems to be three possible contributing factors to an enriched/unenriched individual's exploration: motivation/stimulation, current level of information as a result of exploration, and potential behavioural diversity for exploration as a result of experience in home cage. It is important to note that these three are not necessarily mutually exclusive.

In a future study, it would be interesting to look for possible relationships an individual's home cage exploration and testing environment exploration. For instance, although we found no difference between the enrichment groups in exploration duration under test conditions, we could calculate the difference between the two environments. This would give a measure of

whether exploration increased or decreased in the experiment, relative to the home cage control. Moreover, it would have been useful to investigate whether the unenriched birds had reached a ceiling by comparing their exploration at the start and end of each recording. One other concern is with our home cage video sampling method. Although we did not include the first and last hour of each day, or the key feeding period, we randomised the time chosen. Exploration is likely to have a diurnal rhythm (e.g. Gentsch et al., 1982; Vestergaard, 1982), so it not clear we controlled for this. Furthermore, in total each individual was observed within their home cage for approximately 2 hours each. This may not have given us a comprehensive overview of all of the 31 exploratory behaviour categories, or even of each individual with each toy.

5.4.2 Complexity of exploratory behaviours

Not only did the enriched kakariki show a greater diversity of behaviours than the unenriched kakariki under test conditions, but also, as hypothesised, more complex exploratory behaviours. The unenriched kakariki were more likely to display simple or intermediate exploratory behaviours. This exploratory complexity result supports the argument that the enriched kakariki were more motivated to explore and were more experienced with a wider range of objects and affordances* than unenriched kakariki. Hence, they had greater experience of using different and more complex behaviours to gather information.

By performing more behaviours on an object, these enriched kakariki were *potentially* better able to solve a problem-solving task than the unenriched kakariki. The complex toys in the enriched enclosures were designed

to encourage problem-solving, or more flexible, innovative behaviour, such as to get a nut out of a transparent box. Nonetheless, we did not directly measure cognitive performance or problem-solving ability, so further studies are needed to verify this. Sol et al. (2011), for instance, found that mynah birds (*Acridotheres tristis*) living in urbanised environments were better at problem-solving than mynahs in rural environments. The authors attributed this to there being fewer costs (e.g. predation) associated with exploration in urban environments. This is likely to be an important factor, but the evidence here suggests the urban environment also provides a wider variety of object properties than the rural environment, thus providing urban birds with a larger 'tool-kit' of potential problem-solving strategies.

What is not clear is whether certain behaviours were employed under certain circumstances. An enormous amount of information confronts a kakariki's senses from moment to moment, but not all of it is relevant (Arriola-Rios et al., 2013). It is not apparent how they process and store this information within a brain of finite capacity, nor what types of cues kakariki attend to in the environment in preference to other cues (e.g. colour, texture, or shape). It is likely that the complex toys in the enriched enclosures provided more functional* or causal information about the physics of the surrounding world (e.g. how cogs turn in relation to each other), than the simple toys in the unenriched enclosures. The latter items only provided information about the properties of ropes and wooden perches, such as object rigidity versus compliance. Mettke-Hofmann et al. (2006) investigated the impact of object complexity on exploration in garden warblers (*Sylvia borin*). They found that the warblers touched a complex object significantly later than a simple object. They argued that although the complex object could provide more causal in-

formation, it would take longer to explore than the simple object. It would also be more likely to hide a threat than a simple object, thus it was initially avoided.

5.4.3 Object type and novelty effects

Object type and novelty had an impact on the exploration of kakariki in both housing conditions. In the home cage, the enriched individuals focussed on the toys more than the other cage features (e.g. mesh, perches or water bowl), whereas, as expected, there was no difference between the two for the unenriched individuals. In the behavioural tests, the enriched group were quicker to approach an object and begin exploring it than the unenriched group, but as predicted, this was dependent on whether the object of interest was novel or familiar to the individual. In both groups, a novel object resulted in a longer latency to the first exploration bout than a familiar object. However, the enriched individuals were quicker to approach a novel object than the unenriched individuals.

This relationship between object novelty and exploration has been found for a range of species in a range of contexts (e.g. Wood-Gush and Vestergaard, 1991; Hughes, 1997; Greenberg and Mettke-Hofmann, 2001; Pisula and Stryjek, 2006; Bunzeck et al., 2010). Novelty can induce exploration, as the animal seeks to gather more information about the unknown, according to their level of uncertainty (Hughes, 1997; Inglis and Langton, 2006; Beck et al., 2008; Koehler and James, 2009). However, this is often preceded by another survival instinct: neophobia; a fear of the unknown and the potential threat it poses. Often the motivation to avoid a novel item and the motivation to explore it can occur simultaneously (Heinrich, 1995; Greenberg and Mettke-

Hofmann, 2001). The unenriched kakariki had not been exposed to as great a range of novel objects as the enriched kakariki, so they were not as accustomed to novel toys posing no threat. This meant that under test conditions their neophobia seemed to dominate their neophilia and the motivation to gather information about the unknown, resulting in a longer latency to the first exploration bout than the enriched kakariki.

The type of the home cage toys also seemed to be important for the amount of exploration. This may just be because of the novelty effect, since in the enriched condition, the toys were rotated on a weekly basis between the cages. Although their position within the cage did change week-to-week, the type of toys in the unenriched condition remained the same. Alternatively, this result may be due to the greater range of affordances/properties the toys provided in the enriched condition. In considering the kakariki's particular ecological niche, further studies are needed to see which properties of enrichment devices are particularly important for an individual's exploratory behaviour. For instance, the work by Kim et al. (2009) and Webb et al. (2010) investigated the orange-winged parrot's preferences for particular object properties. These studies provide a potential model for extending this research question to kakariki..

5.4.4 Animal welfare implications

Captive animal welfare has become a priority for scientific government policy and research funding in recent years. As a result, thorough housing and management guidelines have been published for keeping different animal species for research purposes, which are enforced by the UK Home Office. It has been acknowledged in recent years that it is important not only to meet the

basic physical welfare needs of a captive animal, but also its different cognitive needs (e.g. Brydges and Braithwaite, 2008; Clark, 2011). However, there are surprisingly few species-specific guidelines for housing birds in scientific policy or legislation, even though they make up approximately 25% of animals used in research in the EU, and more than 100,000 procedures are carried out on birds every year under the UK Animals (Scientific Procedures) Act 1986 (Hawkins et al., 2001). Among birds, psittacines are distinctive for their intelligence, anatomy and sensory capacities, so their confinement for research purposes in a variety of fields is increasing, yet there are few enforced guidelines to maintain either their physical or cognitive welfare in captivity (Evans, 2001; Kalmar et al., 2007, 2010).

In this chapter, we have shown unenriched kakariki explored less than enriched kakariki. This may not necessarily indicate poor welfare, especially as none of the kakariki displayed any abnormal or stereotypic behaviours (van Hoek and ten Cate, 1998; Evans, 2001; Garner et al., 2003, 2006; Lumeij and Hommers, 2008) and the unenriched birds resumed 'normal' levels of exploration in their behavioural tests. However, as both in the home cage and under test conditions, the unenriched individuals did not display the same behavioural diversity as the enriched individuals, perhaps their welfare was not as good as it could be. This is evidence that a few easy and economic means of enrichment can have a positive impact on a parrot's behavioural repertoire and, by extension, their cognitive well-being. For instance, rotation of the toys or other enrichment devices between cages on a weekly basis is an easy means of increasing natural activity patterns.

We also found that unenriched individuals had longer latencies to ap-

proaching novel objects. This could result in a need for more habituation trials and the test trials lasting longer. This might mean that not as much behavioural data could be collected as with enriched individuals. In other words, neophobia in chronically unenriched birds could reduce the productivity of cognitive and behavioural tests (Newberry, 1995; Shettleworth, 2009). For instance, perhaps an apparent lack of cognitive capacity for a particular skill in a sample population is just due to too much neophobia overwhelming the tendency to explore (e.g. Wood-Gush et al., 1990).

5.4.5 Summary

We have shown how a few small changes to an animal's environment can have a large impact on behavioural diversity and exploration patterns. We have also considered how object novelty and complexity can affect exploration and neophobia. Consequently from this preliminary study, we can begin to reason about what type of information may be available for an individual to gather through exploration. Our results suggest that enrichment could be a means of exploring the different limits of cognitive capacities in different ecological niches. This is a distinctive approach that previously has not been greatly utilised. Our conclusions are tempered though by the observation that all of our results are based on captive, rather than wild, birds. Nonetheless, our findings have housing implications not only for other bird species, but also other animal groups, such as rodents (Mench, 1994).

So far this thesis has outlined how an animal's sensorimotor system may be adapted for exploration and how the environmental information they gather impacts upon it. This begs the question of how this information may be represented and supported in an animal's brain (Demery et al., 2010; Arriola-

Rios et al., 2013). Many more details still need to be investigated, such as what specific environmental cues an animal focusses upon, and how do different exploration strategies change with time. Perhaps the animal has particular cognitive and behavioural adaptations for solving particular environmental problems.

These are some of the issues that will be discussed in Part III, where we will consider how different exploration strategies may be exhibited in an animal's behaviour, supported by various underlying cognitive learning mechanisms. We will test different aspects of these strategies by observing exploratory behaviour in kakariki in more detail in chapter 6. We will further investigate these ideas through a series of comparative exploration tests in human children in chapter 7.

Part III

Cognitive & Behavioural Strategies During Exploration

CHAPTER 6

Exploratory learning strategies in parrots

Material from of this chapter has formed part of three publications (Demery et al., 2010; Chappell et al., 2012; Arriola-Rios et al., 2013).

The majority of animal cognition research has focussed on establishing what cognitive capacities of different species are, rather than how animals acquire and structure information to support learning, specifically through exploratory behaviour. We argue that exploration in humans and non-human animals is not random; but structured, selective and sensitive to particular categorical features of the environment. We have exploited the natural exploratory tendencies and unique sensorimotor apparatus of parrots to investigate the mechanisms of learning about objects and their affordances through vision and manipulation. Several object properties were selected as being important to a kakariki's environment, such as weight and compliance. A series of simple behavioural experiments focussing around these properties allowed a detailed analysis of the exploration process. Kakariki explored more when there were novel, functional or unexpected changes in the environment. We conclude that this, among other findings, reveals that kakariki do seem to have certain structured exploration strategies. Finally, we discuss the implications of our findings for other animals, including humans, from the perspective that some exploratory animals form, test and refine their hypotheses about the world throughout their lives (Demery et al., 2010; Arriola-Rios et al., 2013).

6.1 Introduction

EXPLORATION and play* in animals have puzzled biologists for decades: they are expensive both in terms of time and energetic resources, yet they have no immediate fitness benefit to the animal (Power, 2000). An exploring animal exposes itself to the risk of predation, potential consumption of toxic items, and expends precious metabolic energy (Archer and Birke, 1983). Its time could instead be spent on other more fruitful behaviours with clearer benefits, such as foraging or courtship (Ficken, 1977; Bekoff and Byers, 1998). Nonetheless, exploration is found throughout the animal kingdom in a range of environmental contexts (e.g. Berlyne, 1960; Glickman and Sroges, 1966).

Upon casual observation, exploration has little form or structure. Indeed, many thought it was just a byproduct of seeking nominal stimulation in the absence of other more important biological drivers, like foraging (e.g. Miller and Dollard, 1941; Harlow et al., 1950). Nonetheless, a general consensus has been reached that it is important for the gathering of information and learning, whether it is to gain knowledge about novel objects, food, mates, predators or shelter (Archer and Birke, 1983; Renner, 1990).

There are two schools of thought regarding the function of exploratory object manipulation: that its function is proper motor development, or that its function is proper cognitive development (e.g. Byers and Walker, 1995; Power, 2000). In support of the motor development theory, there is evidence that exploration occurs more in species that need to practice and develop the motor skills necessary to perform complex manipulations of food items (e.g. birds-of-prey or extractive foragers; Negro et al., 1996; Gamble and Cristol,

2002; Visalberghi and Neel, 2003; Auersperg et al., 2011), or items for building various constructions (e.g. the courtship bowers* of bowerbirds, Ptilonorhynchidae; Collis and Borgia, 2010; Hansell and Ruxton, 2008). Exploration in these species further occurs more frequently in times of hunger (Hall and Bradshaw, 1998; Pellis, 1991). However, if exploratory object manipulation were just for training motor skills, then it should rarely occur after these skills are acquired in juvenescence and thus rarely be found in adults. Indeed in some species this does seem to be the case. The neophilia* and object exploration displayed by juvenile ravens (*Corvus corax*), for instance, almost disappears one month post-fledging (Heinrich, 1995; Kijne and Kotrschal, 2002).

However, in many species where neophilia recedes upon maturity, exploration continues to operate (Power, 2000). Despite the presence of abundant resources or means-of-escape, exploration in these species can even be triggered by unknown threatening stimuli (Murphy, 1978). For instance, Inglis and Shepherd (2010) found rats (*Rattus norvegicus*) preferred to work to gather information about a rare, poisonous food item, despite the presence of familiar, safe food. However, this study is also an example of how the motivation to gather information is often closely intertwined with the innate drive to maximise feeding opportunities.

In other animals, neophilia persists throughout adult life (e.g. parrots; Luescher, 2006). These species are characterised by altricial development*, long lives, generalist foraging mode and large social groups (Ficken, 1977; Ortega and Bekoff, 1987). This has led researchers to highlight the importance of exploration for cognitive development and innovation (e.g. for tool use; Beck, 1980). These types of species need exploration to continually learn

and extend their knowledge about the world throughout their lives (Gibson, 1988; Chappell et al., 2012). This may allow them to prepare for unexpected events, frequently found in unpredictable, variable environments (Bekoff and Byers, 1998). For instance, Verbeek et al. (1994) found that individual differences in great tits' (*Parus major*) exploratory style* (i.e. quick versus thorough) predicted sensitivity and behavioural responsiveness to environmental changes (e.g. searching for food location).

Clearly though, proper cognitive development cannot occur without proper motor development, and vice versa (Bushnell and Boudreau, 1993). Animals need to move around and interact with objects in order to explore, so separating the putative functions is likely to be difficult, and ultimately not very revealing. Assuming that exploration *is* for gathering information (of any kind) about the world, what is more compelling to investigate is how exploratory behaviour is *structured* to support learning.

Despite the prevalence of exploration throughout the animal kingdom, there has been surprisingly little systematic, quantitative research on the form of exploration – whether it is actually unstructured, as the early biologists thought it might be, or if it is to some extent organised(for a review see Renner, 1990). An animal must balance the amount of useful, relevant information obtained from its vast surroundings against the energy expended in gaining it (Chappell and Sloman, 2007). Structured exploratory behaviour strategies, supported by specific sensory and motor predispositions, would allow the animal to gather and process information efficiently (Chappell et al., 2012; Arriola-Rios et al., 2013).

What systematic research there is, has largely been anthropocentric*, coming from the field of human developmental psychology (Povinelli, 2004). Here it is widely accepted that children construct knowledge about their surrounding world by actively exploring and interacting with objects in their environment (e.g. Piaget, 1929; Gibson, 1988; Caruso, 1993; Hirsh-Pasek, 2008). For instance, Ruff (1984; 1986) found that the types of manipulation infants used altered depending on how the affordances* of a series of objects changed.

Fewer studies have looked at the structure of object exploration in non-human animals (Weisler and McCall, 1976; Inglis, 1983; Renner and Pierre, 1998; Power, 2000). The only quantitative result is that across many species any form of novelty results in a longer exploration time (for a review see Wood-Gush and Vestergaard, 1991; Heyser and Chemero, 2012). Exploration has also been extensively investigated as a behavioural indicator of captive animal welfare (e.g. chapter 5; Newberry, 1995; Meehan and Mench, 2007; Clark, 2011). Primatologists have investigated object exploration from a developmental view-point (e.g. Hayashi and Takeshita, 2006; Matsuzawa and Tanaka, 2006; Bard, 1995; Chevalier-Skolnikoff, 1977), or investigated how information is cross-modally* transferred (e.g. Gunderson et al., 1990; Davenport et al., 1975). However, none of these studies have specifically investigated the structure of exploration.

Otherwise, the non-human literature has largely focussed on the laboratory rodent as a model animal. For instance, rats alter the speed and pattern of their whisking behaviour* to increase information about shape and texture of objects (Grant et al., 2009). The relative frequencies, sequences and complexities of rats' different exploratory behaviours displayed vary according

to previous experiences and object characteristics (Renner and Rosenzweig, 1986; Renner and Seltzer, 1994). A recent study on exploration activity levels in mice (*Mus musculus domesticus*) illustrated how the functional* properties of an object (i.e. 'affordances'*; what actions can be perceived and performed on the object) can often be more important than the physical object characteristics (e.g. size, colour, material; Heyser and Chemero, 2012). These studies suggests rodents' exploratory behaviour is structured in such a way as to increase the quantity and quality of information gained (Chappell et al., 2012).

Not all of the literature has been concerned with primates or laboratory rodents. For example, Kuba et al. (2003; 2006b) has described how the pattern of exploration changes with time and according to the object type in octopi (*Octopus vulgaris*). Among birds, Mettke-Hofmann et al. (2006) has described how exploration in garden warblers (*Sylvia borin*) is influenced by object complexity and experience. The cognitive flexibility* and innovation exhibited by the kea (*Nestor notabilis*) is argued to be partially due to its neophilia and 'playful exploration' of different object affordances (Diamond and Bond, 1999; Gajdon et al., 2011). Each of these animals inhabit unpredictable, variable environments, where it is adaptive to gather information by structured exploration in order to solve any novel problems that may arise (chapter 5; Arriola-Rios et al., 2013).

The majority of animal cognition research, while revealing, has focussed on establishing what the cognitive capacities of different species are (see reviews in Shettleworth, 1993; Thomas, 1996), rather than on how animals acquire and structure information to support learning. There is a tendency to label learning mechanisms according to rather ill-defined concepts and to

group them into one of two categories; such as 'simple associative learning'* versus 'complex causal reasoning'* (Chappell and Hawes, 2012a). It is difficult to discriminate between such labels, as they often overlap depending on the problem the individual is trying to solve and what the target object of interest is. This is particularly problematic given the range of environmental problems faced by different species and different individuals in different ecological niches (Penn et al., 2008).

For example, New Caledonian crows (*Corvus moneduloides*) make tools out of sticks and leaves to fish larvae out of holes (Hunt, 1996, 2000). Laboratory evidence suggests they may be able to select sticks that are of the appropriate size for the specific size of the hole they face (e.g. Chappell and Kacelnik, 2002). One explanation is that a crow may only succeed in selecting the appropriately-sized stick after considerable trial-and-error (a 'simple' learning mechanism; e.g. Bluff et al., 2007). Alternatively, the crow may be able to causally reason about its surroundings and select a stick spontaneously within one trial (a 'complex' learning mechanism; e.g. Taylor et al., 2009b).

These explanations are interesting, but each misses out all of the rich detail of how the crow went from A to B – how it gathered, processed and learnt the information required to fish the larvae out of different sized holes; as well as what the potential influencing social factors were (for a preliminary discussion see Bluff et al., 2010). It is likely the crow uses a combination of learning mechanisms to attain this sophisticated-looking behaviour, but a chimpanzee (*Pan troglodytes*) performing the same behaviour (for a review see van Schaik et al., 1999), may be accomplishing it through quite different

means, given its different sensorimotor* apparatus for perceiving and manipulating tools (e.g. Demery et al., 2011).

Instead of assigning dichotomous cognitive labels to species, we propose more attention should be paid to studying exploration, which provides a window into the variety of attributes different species exhibit. For instance, we can ask if an information-processing organism strategically focusses its exploratory behaviour on particular salient cues, or if it targets particular exploratory action sequences in particular contexts. This may give us an insight into what the potential underlying learning mechanisms may be for processing different *types* of information. By observing exploratory behaviour, we can more systematically frame what an individual is doing and what possible information they are collecting. Then we can describe what specific behavioural features they have, form more concrete experimental hypotheses, and begin to discuss how the behavioural data might fit into different potential learning mechanisms, or perhaps form new cognitive models (e.g. Arriola-Rios et al., 2013).

By observing different animals' exploratory behaviour, we wanted to consider what cognitive adaptations they may have for processing and gathering information. Specifically, we investigated how various object properties influence the pattern of exploration in New Zealand red-fronted parakeets or kakariki (*Cyanoramphus novaezelandiae*). The kakariki provides a useful model for studying exploration, as they have dextrous manipulatory abilities and are neophilic throughout their lives (Smith, 1975; Funk, 2002; Luescher, 2006).

Kakariki have a highly generalist diet and they use the same method of extracting seeds as found in nearly all Psittaciformes (Collar, 1997; Greene, 1998). They can be found at all strata of temperate rainforests, but they are also resident to scrub and grassland habitats (Boon et al., 2001; Kearvell et al., 2002). As discussed above, animals seem to vary their exploration according to a variety of object characteristics, including both visible, physical features and invisible, functional features (e.g. mice in Heyser and Chemero, 2012). This led us to focus our investigations on five object properties through five experiments, which are likely to be important to kakariki in their environment:

1. surface transitions;
2. shape complexity;
3. colour versus centre-of-gravity cues;
4. symmetry versus balance cues;
5. compliance changing over time.

Firstly, a species' sensorimotor system is likely to be adapted to attend to specific information important to their particular environmental niche, such as regularities providing information about different objects' affordances (Gibson, 1977, 1988). A related psittacine, the budgerigar (*Melopsittacus undulatus*), has been shown to attend to edge cues in preference over other visual cues like colour (Bhagavatula et al., 2009). Thus, salient cues that the kakariki may first attend to are the corners and edges of objects, as different surface transitions can cue different object properties (e.g. Taylor and Zwaan, 2010). This gave rise to our first hypothesis:

- across a range of object types, the kakariki will perform more explorat-

ory behaviours on the corners and areas of high curvatures of objects, as opposed to smooth, flat surfaces.

Subsequently, the number of surface transitions available to explore are inherently determined by the complexity of the object. As with human children, kakariki exploration is likely to be influenced by object complexity (Switzky et al., 1974). However, compared to a simple object, a complex object is simultaneously more likely to contain a lot of information and potentially hide a threat (Mettke-Hofmann et al., 2006). Therefore, as an object's shape becomes more complex, we predict that:

- exploration (amount of exploration time and the diversity of exploratory behaviours) performed on it will increase;
- the latency to the first haptic exploration bout will also increase.

Next, we wanted to verify the object's novelty effect, found in other animals, in kakariki (e.g. Wood-Gush and Vestergaard, 1991). However, not all aspects of novelty may be equally salient to kakariki (as with humans and mice in Perone et al., 2008; Heyser and Chemero, 2012). It is adaptive for an animal to focus on exploring functional cues (e.g. weight) over solely aesthetic cues (e.g. colour), as functional cues are likely to provide more information about how an object may behave (Chappell et al., 2012).

Hence, we investigated the relative importance of visible cues (e.g. colour, shape, symmetry) versus invisible, more functional cues (e.g. centre-of-gravity*, balance) by manipulating the object properties the kakariki were exposed to over two experiments. Greater exploration can ensue after an

object behaves differently to expectations (e.g. Schulz et al., 2008; Arriola-Rios et al., 2013) and extractive foragers* have been shown to be particularly sensitive to centre-of-gravity cues (e.g. Visalberghi and Neel, 2003; Lee et al., 2012). Therefore, in the third experiment we were particularly interested in varying an object's centre-of-gravity, and hypothesise here that:

- more time will be spent exploring a novel object than the familiar object, but this effect will decay over time;
- more exploration will occur with changes in an object's more functional properties (shape and centre-of-gravity) than its more aesthetic properties (colour);
  - this effect will be more pronounced when the functional property change is unexpected and invisible (centre-of-gravity).

In a similar, subsequent experiment, the visible cue we varied was symmetry and the invisible cue we varied was balance. These object properties seemed particularly compelling to investigate considering studies on humans like Zhang et al. (2010) and Crevecoeur et al. (2011), where grip forces* and exploration were modulated by anticipating an object's balance and torque* from the visual perception of its symmetry. Kakariki are a very manipulatory species like humans (Smith, 1975; Funk, 2002; Luescher, 2006). Exploration of an object's symmetry is likely to be related to its shape complexity (as in the second set of hypotheses above). This led us to hypothesise that:

- if the centre-of-gravity is in the expected location, asymmetric objects will be explored more than symmetric objects, especially if the asymmetric object is complex;

- whereas, if the centre-of-gravity is in an unexpected location (as in an unbalanced symmetric object, or a balanced asymmetric object), then objects with this invisible cue will be explored more than other objects just with visible cues of interest (e.g. shape symmetry or complexity).

Finally, categorisation of the world into has been shown to occur in a range of animals (e.g. Shutts et al., 2009; Crouzet and Serre, 2011; Xu, 2011; Soto and Wasserman, 2012; Wasserman et al., 2012). Decomposing a vast, variable environment into collections of object properties, affordances and processes greatly reduces the computational complexity of processing a range of continuous sensory signals (Chappell et al., 2012). Moreover, categorisation enables learning generalisation in novel conditions from a few experiences (Karmiloff-Smith, 1995).

Thus, when animals collect information about a novel object property (e.g. compliance), they seek to partition the information into different categories (Arriola-Rios et al., 2013). We expect they would first focus their exploration on the extreme examples, as these quickly provide general information about the boundaries of different categories (e.g. rigid versus compliant). There are always exceptions to the rule, so it would be adaptive, especially for animals in variable environments, to gradually refine their knowledge, by progressively focussing on the more intermediate examples (Demery et al., 2010; Arriola-Rios et al., 2013). To test this idea, the particular property we chose to investigate was compliance; i.e. the amount an object's surface deflects under pressure or loading. Compliance is probably a particularly salient cue for kakariki inhabiting an arboreal environment, as it is for orang-utans (*Pongo pygmaeus*; discussed in Tecwyn et al., 2012). Compliance

has also been shown to be of great importance to the cognitive development of human infants (e.g. Rochat, 1987; Bourgeois et al., 2005). Thus our last set of hypotheses is as follows:

- initially, kakariki will spend a greater proportion of time exploring the most compliant and the most rigid objects, more than other objects of intermediate compliance;
- however, over time, the kakariki will progressively spend more time exploring the intermediate objects, as opposed to the most rigid and the most compliant objects.

6.2 Methods

6.2.1 General subjects and housing

The subjects used in Experiments 2–5 were 21 adult kakariki (*Cyanoramphus novaezelandiae*; 10 females and 11 males). The sample size and the age of the subjects used in Experiment 1 varied and is detailed in subsection 6.2.4. The kakariki were parent-raised and were sourced from four different breeders in the United Kingdom, so they were probably hybrids with the yellow-fronted parakeet (*C. auriceps*; Boon et al., 2001). Seven of the birds were raised within our captive laboratory environment (all hatched in April – May 2010). Once the chicks were 6 months of age, they were transferred to other cages. The other 14 were delivered from the breeders when they were 3 months of age, then quarantined for 28 days (all hatched April – May 2008).

The kakariki were housed indoors according to guidelines set out in Hawkins et al. (2001) and Kalmar et al. (2007; 2010). They were kept in a temperature-

controlled environment (23 ± 5ºC) on a 12:12 light cycle (dark from 8 pm to 8 am daily; UV daylight light bulbs with a high flicker frequency). The kakariki were housed in pairs in adjoining aluminium cages, each sized 1.83 x 1.22 x 1.22 m. They were cleaned out weekly and fed daily at 11 am on a diet of fresh fruit and vegetables with a parrot seed mix (Parrot Mix Royale, Copdock Mill, Ipswich, UK). Wood chips (Lillico Biotechnology, Surrey, UK), water baths and a range of toys and ropes were provided for general environmental enrichment. However, due to another study, 11 kakariki were housed in a more enriched room, while the other 10 were housed in a less enriched room (chapter 5).

Kakariki are especially social, neophilic and active compared to other psittacines (Pepperberg and Funk, 2005). Their highly generalist diet largely consists of seeds, fruit, leaves, buds, flowers, shoots, and nectar, but also insects, animal remains, tiny stones, as well as seaweed and mussels in coastal areas (Greene, 1988, 1998; Funk and Matteson, 2004; Kearvell et al., 2002). They mature at approximately 9 months and live for 5–10 years. Adult birds were appropriate as study subjects, as unlike other species, kakariki continue to explore beyond juvenescence and throughout their adult lives (Collar, 1997; Luescher, 2006). Indeed, adult animals have been thought to be a more appropriate study subjects than juvenile species for investigating exploration (Rheingold, 1985; Hall, 1998). In this chapter, we are interested in how kakariki structure the information they acquire through exploration, rather than what the different cognitive developmental stages are that they go through (like in Funk, 1996a,b, 2002; Funk and Matteson, 2004).

6.2.2 General materials

The test apparatus was set up on a table within a custom-made test cage (67 x 58 x 60 cm). The experimenter sat on the other side of a solid screen in front of the apparatus to avoid visual cueing. The subjects' behaviour was monitored remotely and recorded via two video cameras (Sanyo Xacti VPC-CG10, recorded using MPEG-1/2 codec, 720x576 resolution, 30 fps) positioned perpendicular to the test cage, above and to the side of it.

Before the experiments, a pilot colour preference test was performed with lengths of rope (similar to that found in their home cages). It was found kakariki were not particularly attracted to or averse to red or blue, and the preferences for red and blue were approximately equal. Therefore, these colours were used for the test objects.

Nearly all of the objects (except for those otherwise described in Experiment 5, subsection 6.2.8) were made out of Polymorph (Mindsets Ltd., Waltham Cross, UK). This is a caprolactone polymer that becomes transparent and mouldable at 60ºC, but at room temperature it becomes opaque and stiffer, stronger and tougher than the polythene used in domestic products. All of the objects were approximately the same size (2 x 2 x 2 cm) and mass (17.2 ± 1.5 g), which could be easily grasped and manipulated by a kakariki. At the beginning of each trial, an outer layer of blue or red Plasti Dip® (Petersfield, UK) was sprayed on the objects. This is an air-dry, non-toxic rubber coating, which allowed recording of the number and position of the indents made on the Plasti Dip layer by the beak and claws.

6.2.3 General protocol

The experiments reported in this chapter were conducted between March 2009 and April 2012. They are presented in the general order they were conducted, except for Experiment 3 (subsection 6.2.6). This was conducted first, three months before Experiment 2 (subsection 6.2.5) to minimise experience effects of balls and cubes. None of the work conducted for this project required a Home Office Licence and all the techniques used were non-invasive, following the guidelines set out by the UK Animals (Scientific Procedures) Act, 1986.

During testing, individual kakariki were presented with a series of simple objects with different properties, then their exploratory behaviour was recorded over 25-minute trials. They had not experienced any of the objects in their home cage, or in a previous test trial before. This formed the basis of five analyses, which investigated the following key object properties: surface transitions; shape complexity; centre-of-gravity; symmetry; and compliance.

A typical trial consisted of a five-minute habituation period, followed by 25 minutes of data collection. Immediately before each behavioural experiments' test trials, the kakariki first experienced three habituation trials with a familiar piece of rope over consecutive days (similar to that in their home cage). The general protocol for the habituation trials was the same as the test trials. The time of day that each individual was moved to the test room was pseudo-randomised between 0900 and 1700 between days. The kakariki were trained to individually enter and exit a portable transport cage (81 x 42 x 61 cm), by means of a food reward (strawberry). To ensure that the birds' attention was drawn to the link between entering/exiting the cage and the

reward a clicking sound (produced by a standard dog training device) was employed to seize their attention. When, infrequently, a net was required to catch the bird, an extra five minutes of habituation was allowed in the test room.

All of the ensuing behaviours were recorded live via remote monitoring using JWatcher Video version 1.0 (Blumstein et al., 2007), according to the ethogram outlined in Appendix C. This consisted of five exploratory behaviour categories, divided into 31 sub-categories. The five main categories were:

- visual inspection (e.g. follow, search);
- grasping (transitory e.g. tap; or prolonged e.g. carry);
- actions (e.g. push, pull);
- modifying objects (e.g. bend, pry);
- relating objects (e.g. insert, hook).

Potentially, the kakariki could have performed the same number and variety of behaviours from the ethogram upon all of the objects described in this chapter. From this data collection, the following measures for each trial could be calculated: frequency of specific behaviours; the first and last behaviour category performed; the time between exploration bouts (separated by 10 seconds or more); total holding duration; and the number of successful grasps. However, in this chapter, we have focussed on more general, overall measures of exploration, in lieu of a wider-ranging discussion about our five analyses of different exploration components. They are as follows:

- exploration duration (out of a possible maximum of 25 minutes);
- number of different exploratory behaviours ('behavioural diversity');
- total number of exploratory behaviours (regardless of type);
- latency to first exploration bout.

6.2.4 Experiment 1: surface transitions

In the first experiment, we investigated how exploration may be influenced by the different surface transitions of an object, such as the corners, curves and flat surfaces. This involved a general analysis across a range of object and apparatus types in a range of experiments, including some that are not reported in this chapter.

Subjects and materials

In this experimental analysis, the sample size and the age of the subjects was not consistent across the object types investigated, although they involved the same birds as in Experiments 2–5. These details are outlined in Table 6.1.

Firstly, all of the 21 objects from the experiments reported in this chapter were included in this general analysis. These are shown in Figure 6.2.3, Figure 6.2.4, Figure 6.2.5, and Figure 6.2.6. As reported in subsection 6.2.1, all 21 kakariki were presented with these objects as adults.

Secondly, the three sets of apparatus from another study (chapter 7) were included in the analysis, as shown in Figure 6.2.1. They were designed for a set of comparative behavioural tests to compare exploration in parrots and in human children. Thus, the 'parrot versions' of the tasks were slightly differ-

Table 6.1 – The sample size details for each object type analysed in Experiment 1, which investigated how exploration may be influenced by the different objects' surface transitions (i.e. corners, curves, flat surfaces). The crosses denote which subjects explored all of the objects in all of the experiments analysed. This included two extra experiments not fully reported in this chapter: the comparative experiment and the developmental experiment. The original 14 kakariki were coded by their cage number and their sex. The 7 chicks were coded by their colour ring, but their sex is included in brackets. The number of objects or sets of apparatus in each experiment are also shown in their respective column title.

Subject ID	Expt. 2 - 6 objs.	Expt. 3 - 5 objs.	Expt. 4 - 5 objs.	Expt. 5 - 5 objs.	Comp. Expt. - 3 app.	Dev. Expt. - 8 app.
1m	x	x	x	x	x	
1f	x	x	x	x	x	
2m	x	x	x	x		
2f	x	x	x	x		
3m	x	x	x	x	x	
3f	x	x	x	x		
4m	x	x	x	x		
4f	x	x	x	x		
5m	x	x	x	x	x	
5f	x	x	x	x		
6m	x	x	x	x	x	
6f	x	x	x	x		
7m	x	x	x	x		
7f	x	x	x	x		
P1(m)	x	x	x	x	x	x
Y1(f)	x	x	x	x	x	x
Y2(f)	x	x	x	x		x
Y3(m)	x	x	x	x	x	x
Y4(f)	x	x	x	x	x	x
Y5(m)	x	x	x	x	x	x
Y6(m)	x	x	x	x		x

ent and smaller than the 'child versions'. Only ten adult kakariki (5 females, 5 males) were exposed to these three sets of apparatus.

The last set of objects included in this general analysis formed part of a periodic series of cognitive developmental tests, based on the tests designed by Uzgiris and Hunt (1989) for human children. This followed a similar protocol to tests run by Funk (1996a; 1996b; 2002; 2004) on New Zealand yellow-fronted parakeets (*C. auriceps*). These objects were exposed to seven kakariki (3 females, 4 males; raised in the enriched cages) during their first 6 months of age. These eight objects are shown in Figure 6.2.2.

Protocol

All of the experiments included in this analysis followed the same general protocol, using the same ethogram (subsection 6.2.3). For each exploratory behaviour category recorded, the associated object part that the behaviour was performed on was also recorded. Although the specific object part was noted, the parts were generalised into surface transitions being either:

- a corner or indent;
- an area of high curvature;
- or a flat, smooth surface.

As each object type clearly did not have a uniform number of each of these different object parts (e.g. balls do not have any corners), the data was pooled across all the object types, rather than being analysed within each object type or within each experiment. The main general measure for this experiment was the total number of exploratory behaviours performed on each ob-

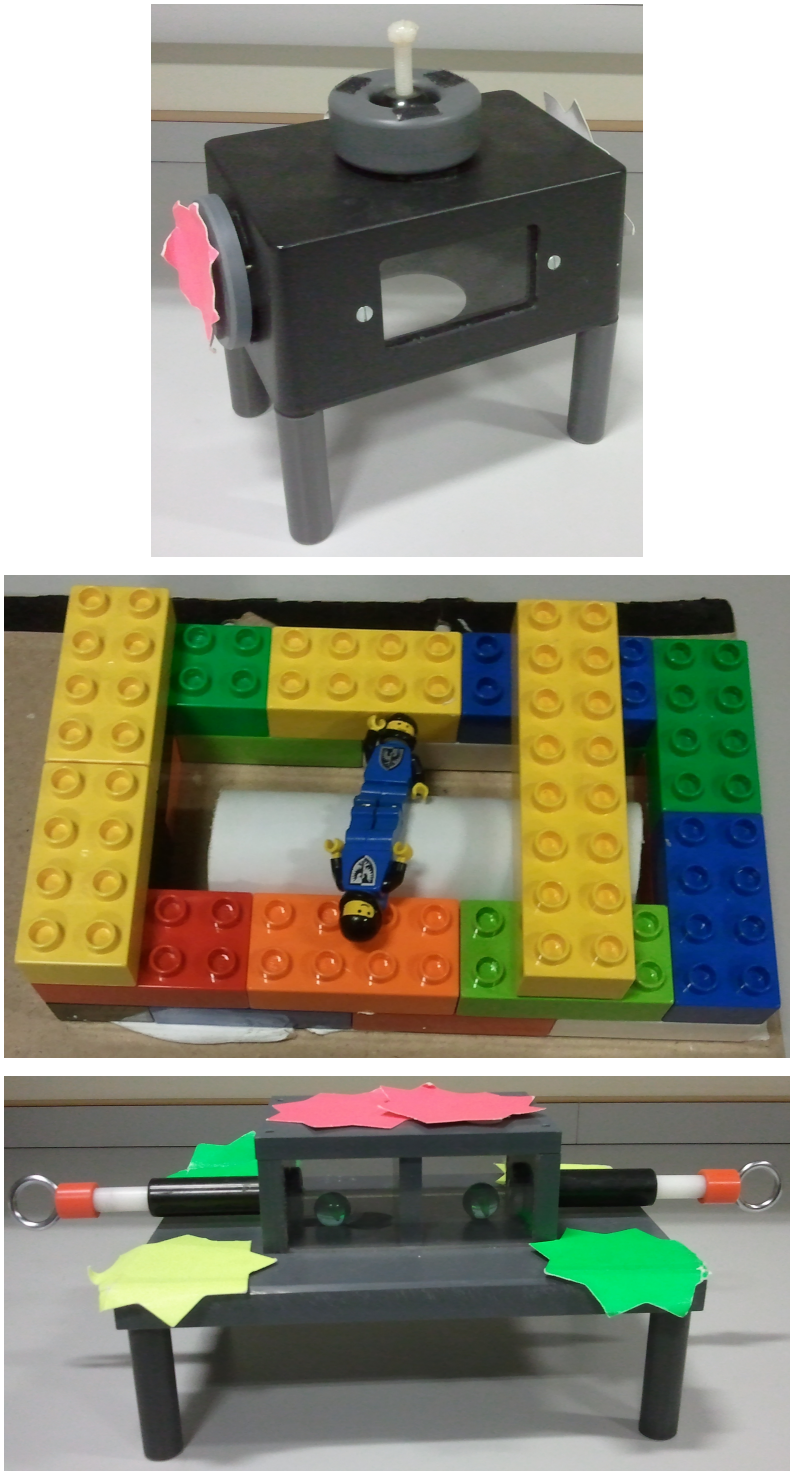


Figure 6.2.1 – This set of three apparatus were exposed to ten adult kakariki (5 females, 5 males) as part of a series of comparative behavioural tests to compare exploration in parrots and in human children. The smaller version of the middle apparatus used for the kakariki was made out small Lego® pieces rather than the large Duplo® pieces (Billund, Denmark). Also the tube with the toy men shown in this figure was replaced by a small transparent tube attached to a hook, with a piece of strawberry inside.

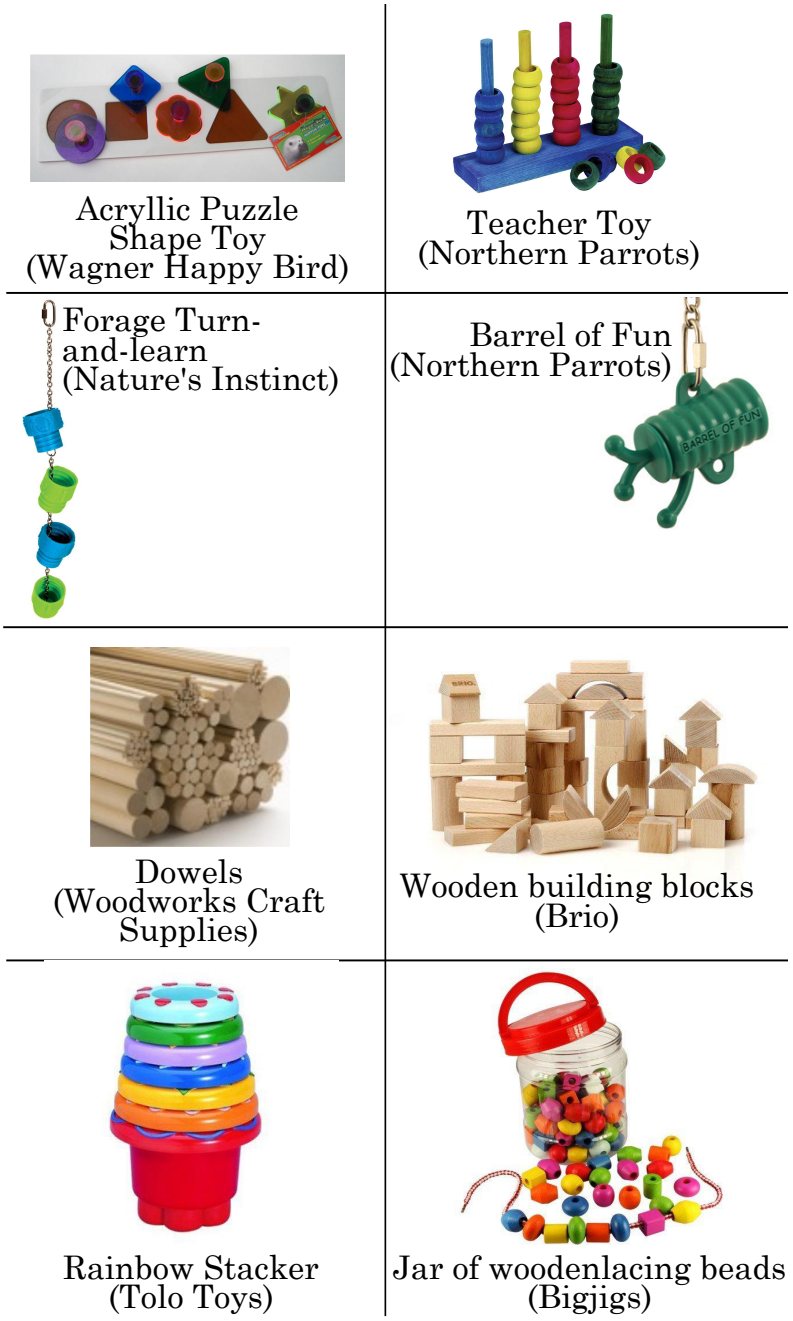


Figure 6.2.2 – These objects were exposed to seven kakariki (4 females, 3 males; raised in the enriched cages) during their first 6 months of age as part of a periodic series of cognitive developmental tests, based on the tests designed by Uzgiris and Hunt (1989) for human children, and similar to those run by Funk (1996a; 1996b; 2002; 2004) on New Zealand yellow-fronted parakeets (*Cyanoramphus auriceps*). They formed part of the analysis in Experiment 1. All of the objects were custom-made or sourced from Northern Parrots (Ramsbottom, UK).

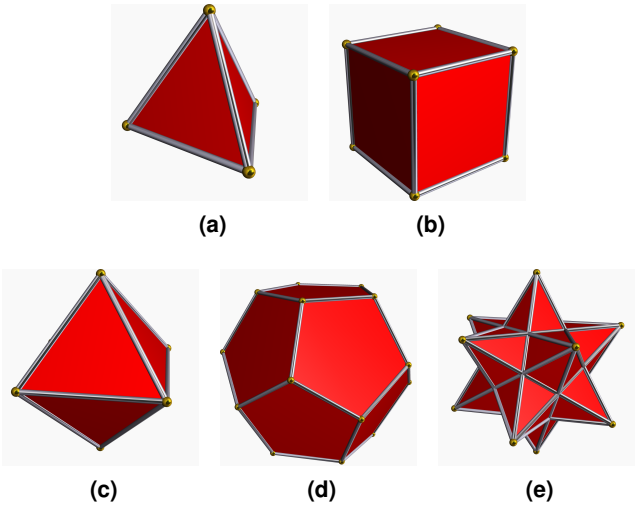


Figure 6.2.3 – Illustrative representations of the different shapes or polyhedra of the objects used in Experiment 2. These illustrations were produced using Small Stella version 4.4 (Webb, 2000), but the actual objects were made out of Polymorph, moulded around solid wooden moulds of the various shapes. The shapes are presented in order of increasing complexity (i.e. increasing number of faces). The most basic shape was a sphere (1 face), then: **(a)** pyramid (4 faces); **(b)** cube (6 faces); **(c)** octohedron (8 faces); **(d)** dodecahedron (12 faces); **(e)** small stellated dodecahedron (60 faces).

ject part, although behavioural diversity was also analysed. Note that these measures were again based on the dataset recorded live, as described above in subsection 6.2.3. The Plasti Dip outer coating aided in the recording of where the majority of the exploration was focussed for each object type, but this within-experiment analysis will not be reported in this chapter.

6.2.5 Experiment 2: shape complexity

Materials

In this experiment, the shape complexity (i.e. number of faces) of the object was varied (Figure 6.2.3). All of the objects were rigid and coloured red. The Polymorph outer layer was moulded around solid (not hollow) wooden moulds.

The simplest shape was a ball or sphere (considered as having 1 face), while the most complex shape was a small stellated* dodecahedron (12 pentagram faces, with 5 pentagrams meeting at each vertex*; Figure 6.2.3e). Essentially, the latter is a three-dimensional regular star, where each face is a concave, regular pentagram. Note that if each pentagram face was considered as 5 triangular faces, then in actuality this polyhedron has 60 faces. This shape is an example of a 'Kepler–Poinsot polyhedron'*.

The other shapes were convex, regular polyhedra* or 'Platonic solids'. This means the faces were congruent, regular polygons and the same number of faces met at each vertex. These were as follows:

- pyramid or 'tetrahedron' with 4 faces (Figure 6.2.3a);
- cube or 'hexahedron' with 6 faces (Figure 6.2.3b);
- octohedron with 8 faces (Figure 6.2.3c);
- dodecahedron with 12 faces (Figure 6.2.3d).

Protocol

The kakariki participated in six test trials over consecutive days. Within a trial, a kakariki was presented with one of the six polyhedra. The order the shapes were presented in was pseudo-randomised, subject to the constraint that no two kakariki experienced the same order of objects. This was designed to minimise practice effects with increasing shape complexity over time.

6.2.6 Experiment 3: visible cues and centre-of-gravity

Materials

The objects in the first phase of the experiment were a novel red ball and a familiar piece of rope (the same type as that found in their home cage). The objects in the second phase of the experiment were allocated to one of four experimental conditions as follows:

- for the control 'no change' condition, the same red ball as in the first experimental phase;
- a blue ball in the 'visible colour change' condition;
- a red cube in the 'visible shape change' condition;
- or a red ball with an awry centre-of-gravity in the 'invisible centre-of-gravity change' condition.

This last item looked the same as the original ball, but was hollowed out with a ball-bearing (chrome steel, hardness grade 100, 10 mm diameter) freely moving inside it (Figure 6.2.4). This caused the ball to roll around unevenly when pushed, and move in a different way to the original ball. However, this also produced small auditory cues.

Note the invisible property (or 'cue/affordances') of centre-of-gravity was also termed as a 'functional' (/'causal') property, because centre-of-gravity affects how the object behaves when interacted with by an individual. The visible property of shape also affects how the object behaved, so it was also termed 'functional'. However, the visible colour property was more an 'aesthetic' than a 'functional' property, as it does not directly affect how the object behaves.

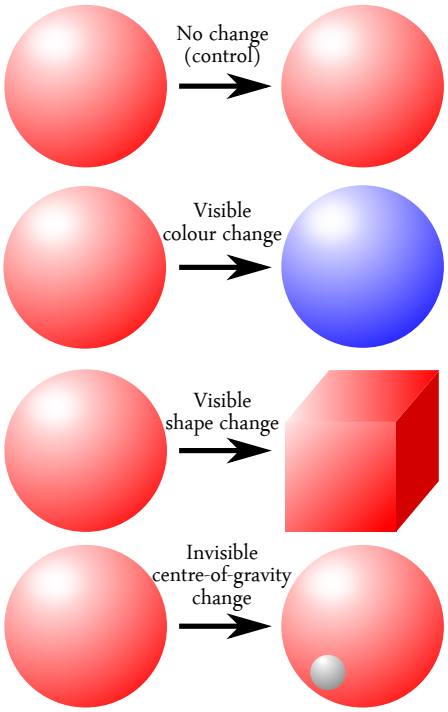


Figure 6.2.4 – A diagram of the conditions of Experiment 3 on visible cues and centre-of-gravity. The kakariki were all first habituated to a red ball over three days. Then on the fourth day they were either presented with: the same red ball (no change condition); a blue ball (visible colour change); a red cube (visible shape change); or red ball that looks the same, but it has a freely-moving ball-bearing inside it (shown by the grey sphere above), making it roll around strangely (invisible centre-of-gravity change). A month later the kakariki experienced this same protocol, but with a different condition; and so on until they had experienced all four objects. In all of the trials, a familiar piece of rope was presented simultaneously with the test object (ball/cube).

Protocol

The first phase of the experiment investigated possible object novelty effects on exploration, while the second phase investigated the relative influence of visible and invisible cues on exploration, if any. The usual habituation procedure with the rope, as found in the other experiments (subsection 6.2.3), was not followed in this experiment. In the first phase of the experiment, all of the kakariki were simultaneously presented with the novel solid red ball and the familiar piece of rope over three consecutive days. The proportion of

the trial time spent exploring each object was recorded.

In the second phase of the experiment, on the fourth day, the kakariki were presented with the same piece of rope and another object depending on which of the four conditions they were in (Figure 6.2.4). All of the kakariki experienced all of the conditions, but in a counterbalanced order. Each condition lasted four days, followed by a gap of a month until the next condition was presented.

6.2.7 Experiment 4: symmetry and balance

Materials

The objects in this experiment primarily varied in their symmetry and balance. Firstly, there were two apparently identical symmetric dumb-bell-like objects, which were either balanced (with a weight embedded in the geometric centre; Figure 6.2.5a), or unbalanced (with a added weight embedded in one of the extreme ends; Figure 6.2.5b) to hold. Note that where the weights were embedded, the objects were solid and not hollowed out like the ball with the awry centre-of-gravity in Experiment 3 (subsection 6.2.6). This meant that the object's centre-of-gravity was either in an expected, or an unexpected location location, according to its symmetry. It is unexpected for a symmetric object to be unbalanced, with its centre-of-gravity to one side.

Secondly, there were two apparently identical simply-shaped, asymmetric objects, which were either balanced (Figure 6.2.5c) or unbalanced (Figure 6.2.5d) in the same fashion as the symmetric objects. It is unexpected for an asymmetric object to be balanced, with the centre-of-gravity in its geometric centre, as opposed to being unbalanced with the weight in its larger end.

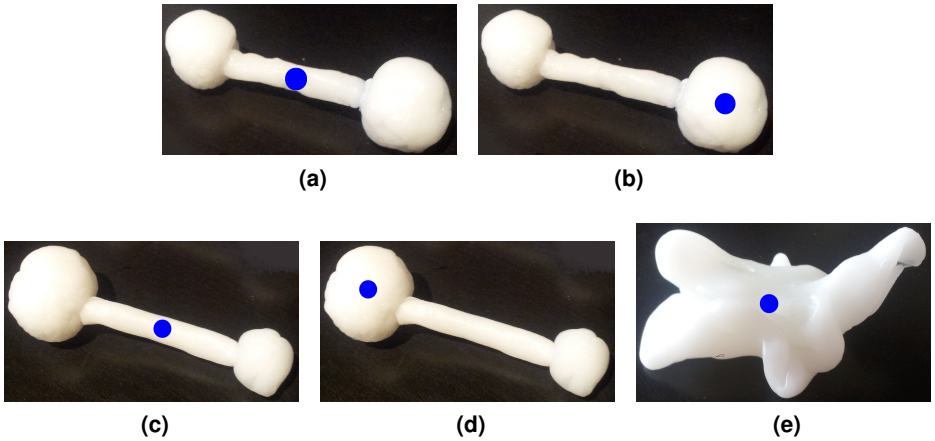


Figure 6.2.5 – The objects used in Experiment 4. Each object was part of a different experimental condition, where symmetry and balance were varied, but also, to a lesser extent, shape complexity. The blue circle in each of the images indicates the position of the embedded weight, which was either in the geometric centre of the object, or in one of the extreme ends. The conditions were as follows: **(a)** balanced symmetric; **(b)** unbalanced symmetric; **(c)** balanced simple asymmetric; **(d)** unbalanced simple asymmetric; **(e)** unbalanced complex asymmetric. Note that in the last condition, while the weight was embedded in the object's geometric centre, its centre-of-gravity was in the left side.

Lastly, there was a irregularly curved, asymmetric object, with quite a complex shape (Figure 6.2.5e). The embedded weight in this object was in its geometric centre.

Protocol

This followed a similar protocol to Experiment 3 (subsection 6.2.6), but the habituation trials with the rope were the same as with the other experiments (subsection 6.2.3). However, in this experiment, the invisible cue was balance and the visible cue was symmetry. Since the birds' spontaneous responses to these cues were of interest in this experiment, there was no familiarisation phase with one of the objects. When the centre-of-gravity was to one side in the target object, its presented position (i.e. on the left or right side when facing the bird) was counterbalanced across trials and individuals.

Firstly, all the kakariki experienced the two symmetric objects and the complex asymmetric object in a counterbalanced order. Secondly, a month later, the kakariki experienced the remaining two objects in a counterbalanced order. These were the two simple asymmetric objects, which were either balanced or unbalanced. They were presented to control for the possible effect of object complexity on exploration, as opposed to the possible balance effect.

6.2.8 Experiment 5: compliance over time

Materials

In this experiment, there were five cubes of different levels of compliance (or 'rigidity'). In a pilot study, the compliance level of each cube was judged blind and agreed on independently by three people. The cubes were all blue, but to create the different compliance levels, they were made of different materials. The most rigid cube (level 1; Figure 6.2.6a) was made of Polymorph, and the next most compliant was made of felt, but filled with sand (level 2; Figure 6.2.6b). Level 3 was a hard sponge (Figure 6.2.6c), and level 4 was a soft sponge (Figure 6.2.6d). The most compliant cube (level 5; Figure 6.2.6e) was made out of felt, but with little stuffing, so it could be compressed very easily.

Protocol

This experiment investigated how exploration of a particular object property (compliance) changed over several days. For five consecutive days, the five cubes were presented simultaneously to the kakariki in a line. The position of each cube in the line changed each day, and the order of each of these positions was randomised between each trial and each bird. Note that it was

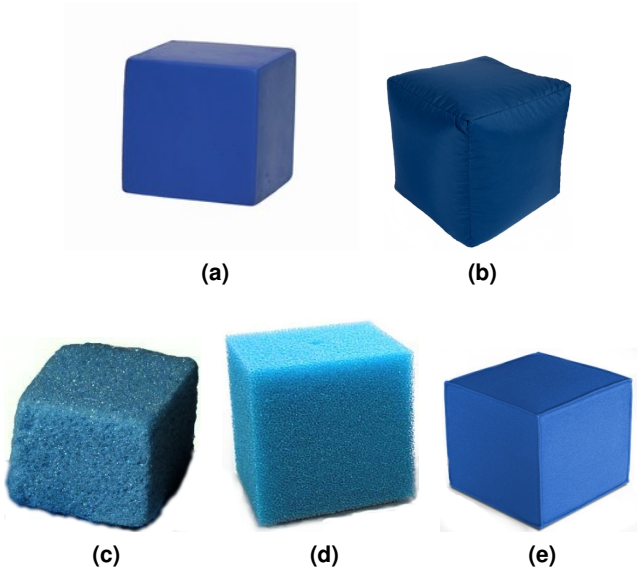


Figure 6.2.6 – The five cubes in Experiment 5 looking at exploration of compliance over time. In order of compliance (level 1 being most rigid): **(a)** rigid plastic cube; **(b)** sand-filled felt cube; **(c)** hard sponge cube; **(d)** soft sponge cube; **(e)** lightly stuffed felt cube. They were all of the same size and presented simultaneously to the kakariki over five days.

not counterbalanced, as there were too many possible combinations for the number of trials run.

The main general measure for this experiment was the proportion of the exploratory time spent on each cube within each trial. There was a potential issue of familiarity with the rigid plastic cube from Experiments 2 (subsection 6.2.5) and 3 (subsection 6.2.6), so this experiment was run at least six months after both these experiments.

6.2.9 Statistical methods

In each experiment, each general measure of exploration (subsection 6.2.3) was analysed using a repeated measures General Linear Model. The assumptions of parametric methods (normality of error, homogeneity of vari-

ance and linearity) were confirmed from plots of coefficients versus fitted values. Where proportional data measures were used (Experiments 3 and 5), the data was arcsine-squareroot transformed. All analyses were performed using Minitab® Statistical Software version 15.1.30. The probability level accepted for significance was $p < .05$.

Where significant effects were found and there were more than two levels within a factor, a series of post-hoc pair-wise Tukey tests were performed to find the source and direction of the significance. In all of the models, in addition each experiment's condition factors (e.g. object type and day number in Experiment 5), the following factors were included to check whether they had an effect on the general exploration measures: sex, age, origin (i.e. breeder or cage hatched in), home cage number and (where necessary depending on the experiment) trial order. As the general key measures were means for each of the 21 kakariki across three test trials, a series of unpaired t-tests were performed on each individual, to check whether the time of day tested and the date tested had an effect on the proportion of time spent exploring. Any deviation from this general statistical method is described in each experiment's protocol above.

6.3 Results

In all of the experiments, there were no significant effects or interactions of sex, origin, cage number, age, time of day, or date on all of the general exploration measures.

Table 6.2 – A summary table outlining the two GLM models for the effect of the type of surface transition of different objects on: the mean total number of exploratory behaviours kakariki displayed within a trial; and the mean behavioural diversity (number of different exploratory behaviours) displayed within a trial in Experiment 1. These means were for each kakariki's mean across all of the object types they explored (across experiments). Sex, origin (10 levels, either breeder or cage ID) and home cage number (1–7) were included in both models as fixed factors, while age was included as a covariate. Surface transition type (corners, curves and flat surfaces) was a fixed factor in both models.

	Factor	d.f.	*F*	*p*
total no. exploratory behaviours	**Surface transition**	**2**	**101.33**	**< .001**
	Sex	1	0.01	0.939
	Origin	9	1.25	0.292
	Cage no.	6	1.35	0.255
	Age	1	0.90	0.348
no. different exploratory behaviours	Surface transition	2	2.68	0.081
	Sex	1	1.06	0.309
	Origin	**9**	**2.24**	**0.038**
	Cage no.	6	2.27	0.055
	Age	1	1.01	0.320

Significant variables are indicated in bold; $n = 63$ for all measurements.

6.3.1 Experiment 1: surface transitions

There was a significant effect of surface transition type on the mean total number of exploratory behaviours within a trial across object types, as illustrated in Figure 6.3.1 (GLM: $F_{2,42} = 101.33$; $p < .001$; Table 6.2). The corners and indents of objects had a significantly larger number of exploratory behaviours performed on them than areas of high curvature (Tukey: $p < .001$) and flat surfaces (Tukey: $p < .001$). Areas of high curvature had a significantly larger number of exploratory behaviours performed on them than the flat surfaces of objects (Tukey: $p < .001$). No significant effect of surface transition type was found on the mean behavioural diversity displayed within a trial

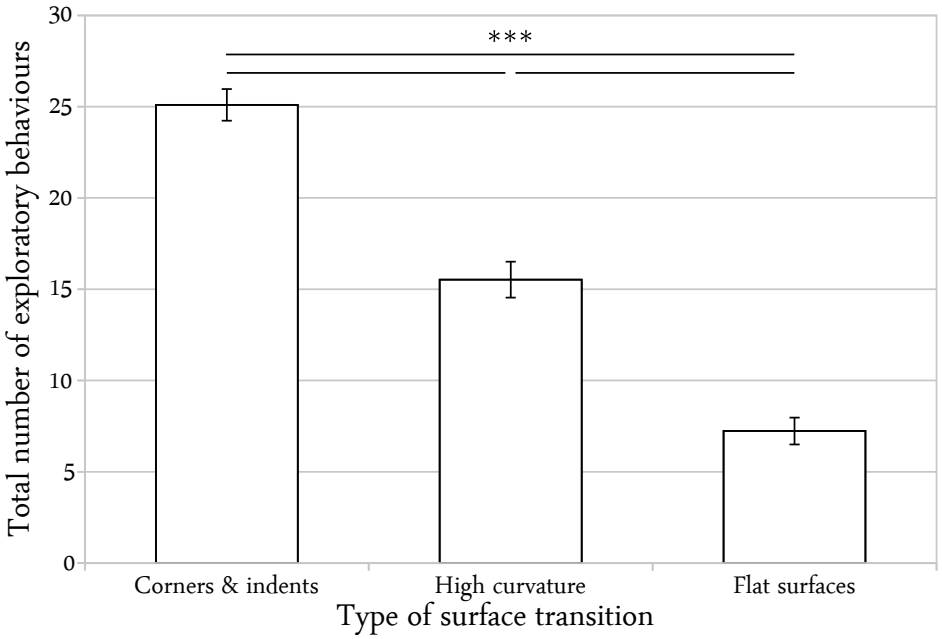


Figure 6.3.1 – A bar chart illustrating the total number of exploratory behaviours kakariki spent exploring (*C. novaezelandiae*) different surface transitions of objects. This was part of a general analysis across a range of object types in a range of experiments conducted between March 2009 and April 2012. So, broadly, the surface transitions were grouped into: corners and indents; areas of high curvature; and flat, smooth surfaces. The sample size and the subjects' age varied between the object types (see subsection 6.2.4 for details). This dataset was based on each bird's mean across all the object types that they explored. The error bars reflect the standard-error-of-the-mean. The line over each pair of bars indicates a significant difference was found between that pair at either $p < .05$ (*), $p < .01$ (**), or $p < .001$ (***; Tukey Test).

across objects types (GLM: $F_{2,42} = 2.68$; $p > .05$).

6.3.2 Experiment 2: shape complexity

The mean of these three general measures of exploration increased with the number of faces of the object: time spent exploring the object (GLM: $F_{5,101} = 32.69$; $p < .001$; Figure 6.3.2a); the number of different exploratory behaviours performed on the target object (GLM: $F_{5,101} = 60.94$; $p < .001$; Figure 6.3.2b); and the latency to the first exploration bout (GLM: $F_{5,101} = 21.27$; $p < .001$; Figure 6.3.3; Table 6.3).

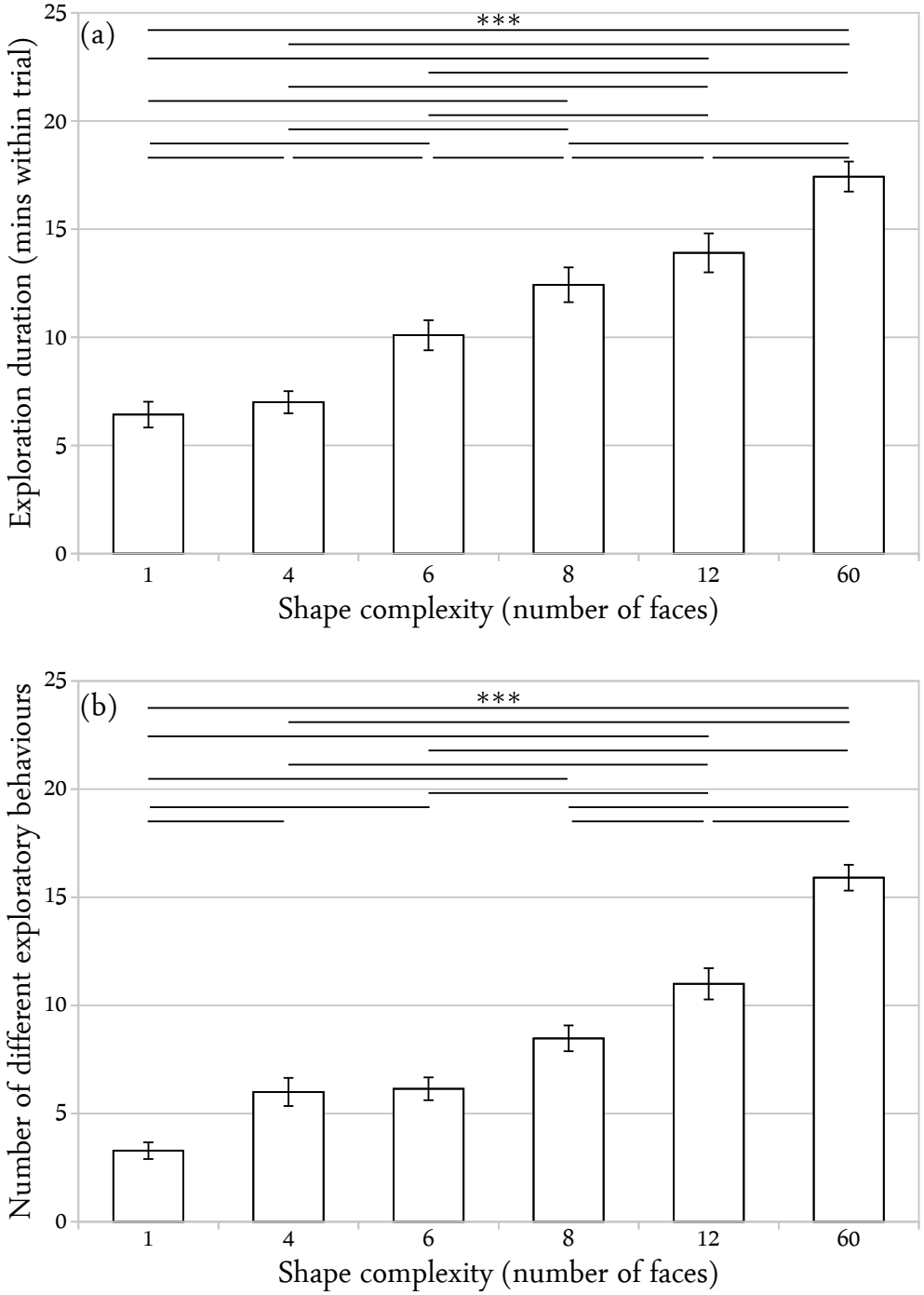


Figure 6.3.2 – Bar charts illustrating the effect of object shape complexity (number of faces) in Experiment 2 against two general measures of within-trial exploration: **(a)** time (minutes) spent exploring the target object; **(b)** behavioural diversity (number of different exploratory behaviours). This was repeated-measures data collected from 21 kakariki within 25-minute trials. One of the six regular, red polyhedra was presented in each trial (shown in Figure 6.2.3). The error bars reflect the standard-error-of-the-mean. The line over each pair of bars indicates a significant difference was found between that pair at either $p < .05$ (*), $p < .01$ (**) or $p < .01$ (***; Tukey Test).

Table 6.3 – A summary table outlining the three GLM models for the effect of object shape complexity (number of faces) within a trial on: time (minutes) spent exploring the object; behavioural diversity (number of different exploratory behaviours); and latency (seconds) to first exploration bout in Experiment 2. Sex, origin (10 levels, either breeder or cage ID), home cage number (1–7) and trial order (3 levels) were included in the models as fixed factors, while age was included as a covariate. The number of faces (1, 4, 6, 8, 12 and 60) was a fixed factor in all three models.

	Factor	d.f.	F	p
exploration duration	**No. faces**	**5**	**32.69**	**< .001**
	Sex	1	0.15	0.699
	Origin	9	0.27	0.982
	Cage no.	6	0.17	0.983
	Trial order	2	0.10	0.909
	Age	1	0.14	0.708
no. different exploratory behaviours	**No. faces**	**5**	**60.94**	**< .001**
	Sex	**1**	**8.19**	**0.05**
	Origin	9	1.36	0.215
	Cage no.	6	2.15	0.055
	Trial order	2	3.19	0.45
	Age	1	1.79	0.184
latency to first exploration bout	**No. faces**	**5**	**21.27**	**< .001**
	Sex	1	0.00	0.955
	Origin	9	0.52	0.858
	Cage no.	6	0.97	0.451
	Trial order	2	0.05	0.951
	Age	1	0.91	0.342

Significant variables are indicated in bold; $n = 126$ for all measurements.

6.3.3 Experiment 3: visible cues and centre-of-gravity

First phase: object novelty

In the first phase of the experiment, the proportion of the trial time spent exploring decreased as the days progressed, whether the birds were exploring the red ball or the piece of rope (GLM: $F_{3,60} = 173.17$; $p < .001$; Table 6.4).

Table 6.4 – A summary table outlining the five GLM models for the object novelty (i.e. object type), day number and type of object property change on: the overall proportion of trial time spent exploring; the mean proportion of exploration time; and the mean behavioural diversity (number of different exploratory behaviour) in Experiment 3. These means were for each day with each cube and were calculated from the 21 kakariki's trials. The proportional time data was arcsine-squareroot transformed. Sex, origin (10 levels, either breeder or cage ID), home cage number (1–7) and trial order (3 levels) were included in the models as fixed factors, while age was included as a covariate. Day number (1–4) was a fixed factor in the first two models. Object type (novel ball and familiar rope) was also a fixed factor in the second model. Lastly, object property (no change, colour, shape and centre-of-gravity) was the key fixed factor in the last three models.

	Factor	**d.f.**	***F***	***p***
overall % trial time exploring$^{\diamondsuit}$	**Day no.**	**3**	**173.17**	**< .001**
	Sex	1	0.77	0.383
	Origin	9	0.59	0.799
	Cage no.	6	0.91	0.491
	Trial order	3	0.96	0.418
	Age	1	0.79	0.376
% exploration time$^{\sun}$	**Object type**	**1**	**289.48**	**< .001**
	Day no.	3	0.00	1.000
	Object type × Day no.	**3**	**48.37**	**< .001**
	Sex	1	0.02	0.851
	Origin	9	0.01	0.987
	Cage no.	6	0.21	0.467
exploration duration$^{\diamondsuit}$	**Object property**	**3**	**50.61**	**< .001**
	Sex	1	0.95	0.333
	Origin	9	0.54	0.840
	Cage no.	6	0.56	0.760
	Trial order	3	0.39	0.760
	Age	1	0.03	0.856
no. different exploratory behaviours$^{\diamondsuit}$	**Object property**	**3**	**6.68**	**0.001**
	Sex	1	0.67	0.416
	Origin	9	0.60	0.792
	Cage no.	6	0.40	0.878
	Trial order	3	0.25	0.863
	Age	1	0.01	0.916
latency to first exploration bout$^{\diamondsuit}$	**Object property**	**3**	**138.50**	**< .001**
	Sex	1	0.04	0.839
	Origin	9	1.06	0.409
	Cage no.	6	1.76	0.123
	Trial order	3	0.15	0.930
	Age	1	0.02	0.879

Significant variables are indicated in bold. $^{\diamondsuit}n = 84$ $^{\sun}n = 168$

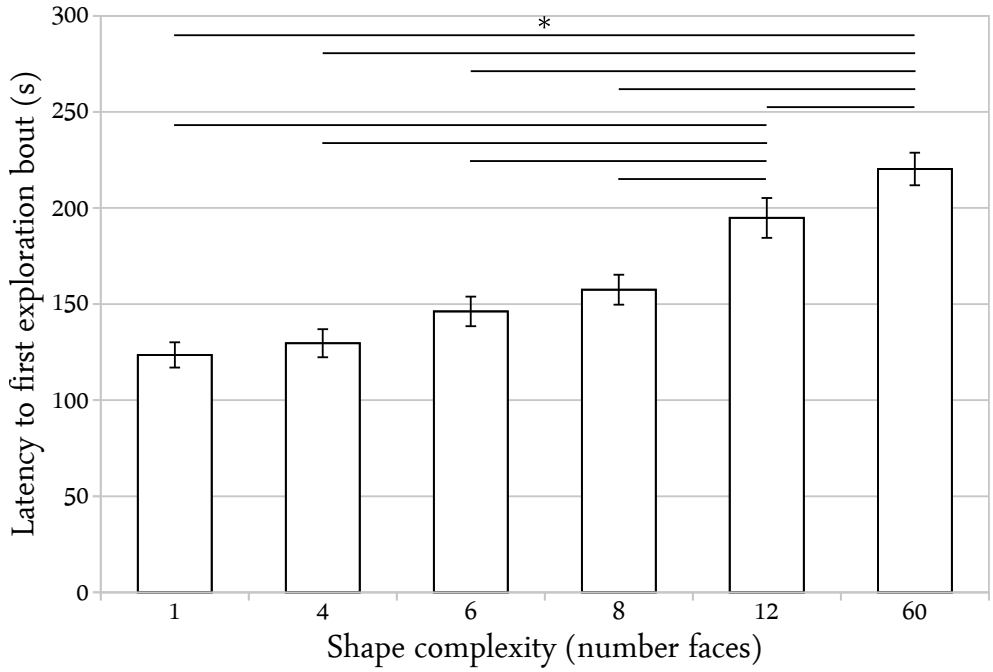


Figure 6.3.3 – A bar chart illustrating the latency (in seconds) to the first exploration bout in Experiment 2 on shape complexity. The bout was defined as having started from the bird's first touch of the target object. This figure caption corresponds to Figure 6.3.2.

The novel red ball was explored for a significantly greater proportion of time within a trial than the familiar piece of rope across the days (GLM: $F_{1,144}$ = 289.48; $p < .001$). There was also a significant interaction between the object type and the day number (GLM: $F_{3,144} = 48.37$; $p < .001$). A series of post-hoc Tukey tests revealed this effect decayed over time, as shown in Figure 6.3.4. On the third day, the significant difference was instead at $p < .01$, rather than $p < .001$ on the first and second day (all Tukey). Note that in the control condition, once the second phase of the experiment started on the fourth day, there was no significant difference between the proportion of exploratory time spent on the red ball on the third day and on the fourth day (Tukey: $p > .05$), although there was a general downward trend from the previous days.

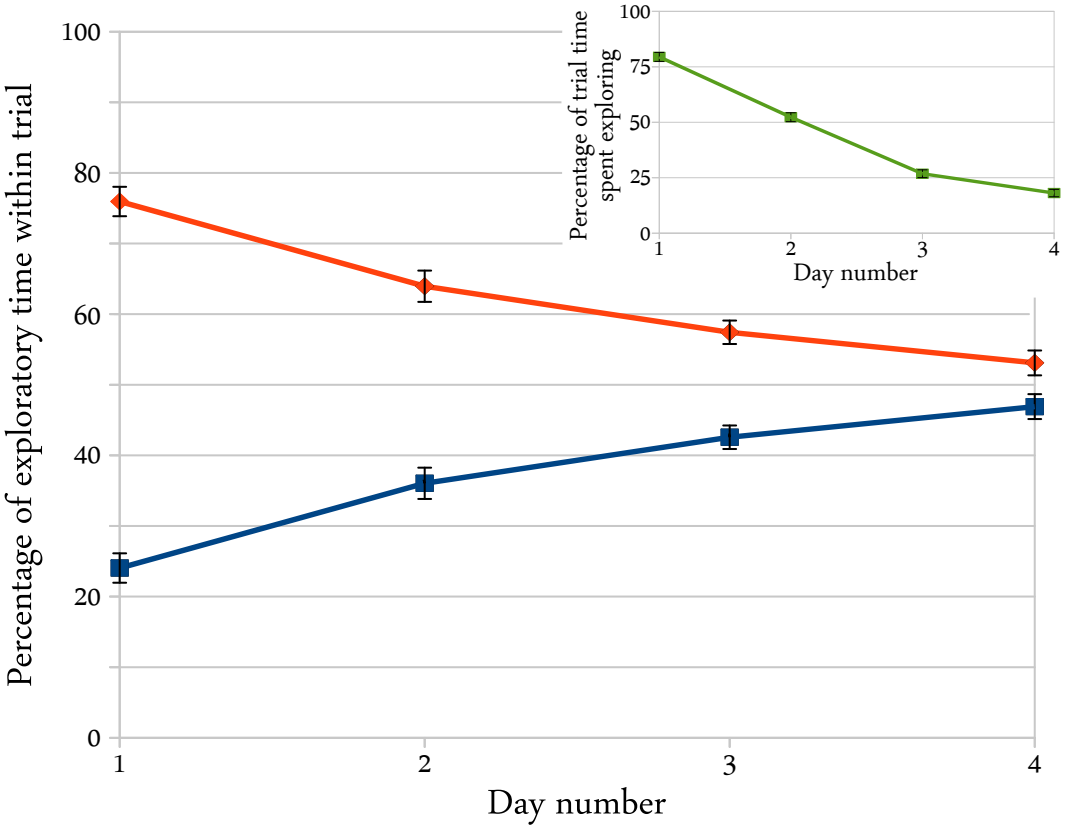


Figure 6.3.4 – Two line graphs illustrating the mean percentage of exploration time within a trial spent with a novel red ball (red line) and a familiar piece of rope (blue line) over four consecutive days in the first phase of Experiment 3. This was repeated-measures data collected from 21 kakariki within 25-minute trials. The mean for each day with each object was calculated from these 21 birds' trials. The fourth day was the first day of the second experimental phase; the data for this day was the control condition when the same red ball was presented. So for some kakariki this did not necessarily follow straight after the previous phase. The piece of rope was familiar, as it was the same type the rope found in the kakariki's home cages. The smaller line graph in the top-right corner shows that overall exploration (pooled across both objects) decreased with each day. The error bars in both graphs reflect the standard-error-of-the-mean. This object novelty effect over the days was found to be significant (GLM: $F_{3,60} = 173.17$; $p < .001$).

Second phase: different cues

There was a significant effect of object property change on the time spent exploring the target object within the average trial (GLM: $F_{3,60} = 50.61$; $p < .001$; Figure 6.3.5a; Table 6.4). Tukey post-hoc tests revealed significant differences between all four conditions to $p < .001$. An invisible centre-of-gravity change was explored for the longest time, followed by the visible shape change, then the visible colour change, and, lastly, the control condition where no change occurred.

A significant effect of object property change was also found for the diversity of behaviours performed on the target object (GLM: $F_{3,60} = 6.68$; $p < .05$). However, post-hoc tests showed a different pattern of effects to the exploration duration, as illustrated in Figure 6.3.5b. Firstly, a significantly greater behavioural diversity was found in the shape change condition, compared to the control (Tukey: $p < .01$) and the colour change condition (Tukey: $p < .05$). Secondly, the centre-of-gravity change condition had a significantly greater behavioural diversity than the control (Tukey: $p < .05$). However, no other significant differences in behavioural diversity were found between the conditions (Tukey: all $p > .05$).

Lastly, object property change had a significant effect on the latency to the first exploration bout (GLM: $F_{3,60} = 138.50$; $p < .001$; Figure 6.3.6). There was no significant difference between the latency in the control condition and in the centre-of-gravity change condition (Tukey: $p > .05$). Nonetheless, the latency was the greatest in the shape change condition (Tukey: all $p < .001$), followed by the colour change condition (Tukey: all $p < .001$).

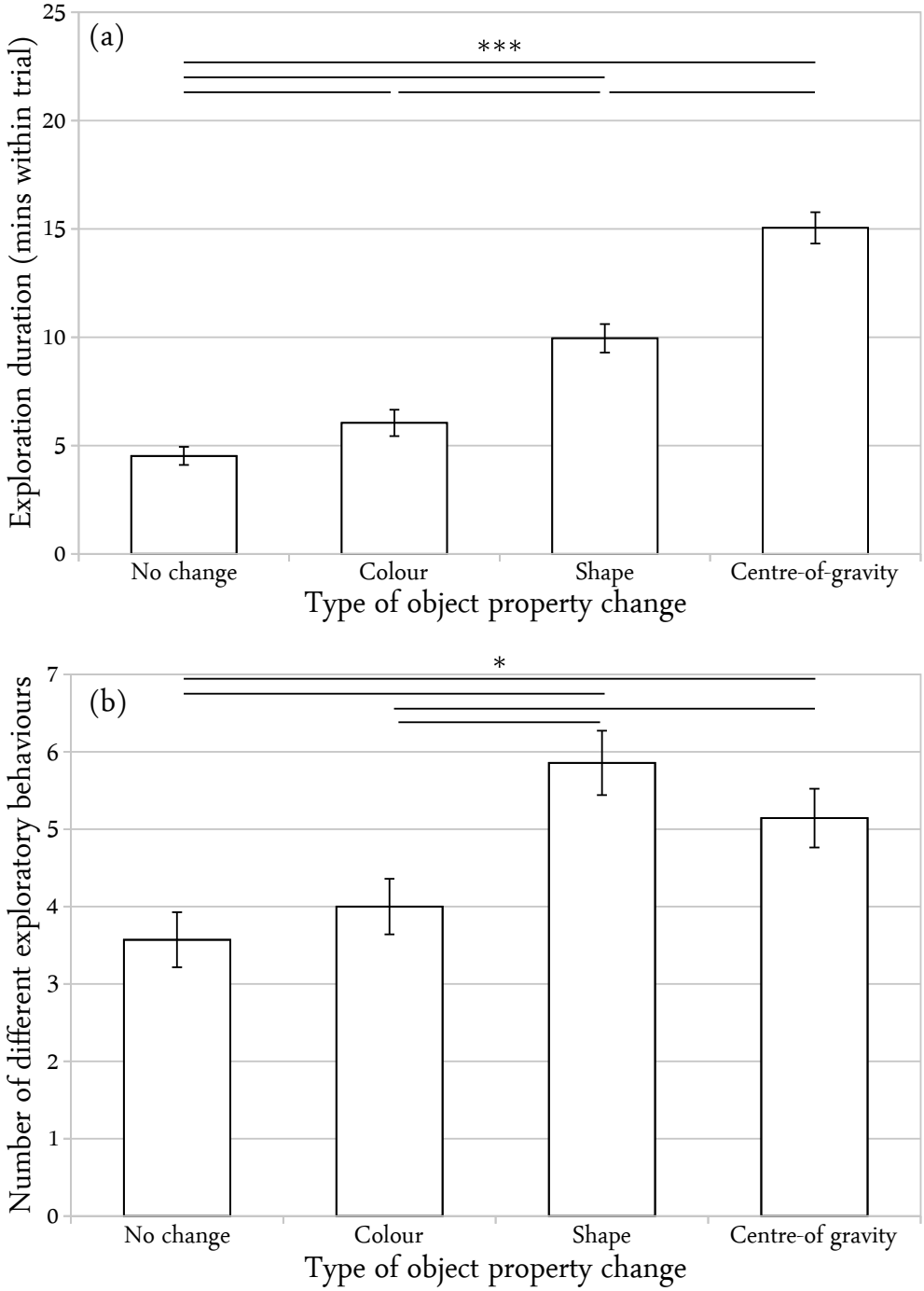


Figure 6.3.5 – Bar charts illustrating the effect of object property changes in Experiment 3 against two exploration measures: **(a)** time spent exploring the target object; **(b)** behavioural diversity. The kakariki were first habituated to a red ball. Then they were either presented with: the same red ball (no change condition); a blue ball (colour change); a red cube (shape change); or red ball with a freely-moving ball-bearing inside (centre-of-gravity change). This figure caption corresponds to Figure 6.3.2.

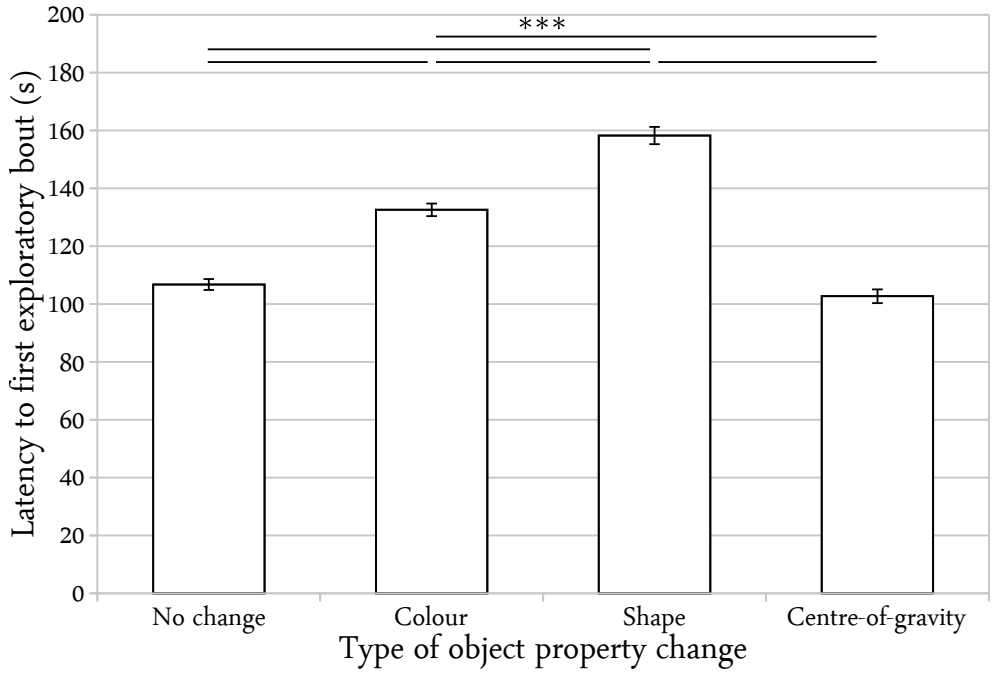


Figure 6.3.6 – A bar chart illustrating the latency (in seconds) to the first exploration bout in Experiment 3 on visible cues and centre-of-gravity. The bout was defined as having started from the bird's first touch of the object of interest. The kakariki were first habituated to a red ball. Then they were either presented with: the same red ball (no change condition); a blue ball (colour change); a red cube (shape change); or red ball with a freely-moving ball-bearing inside (centre-of-gravity change). This figure caption corresponds to Figure 6.3.2.

6.3.4 Experiment 4: symmetry and balance

Object type had no significant effect on the behavioural diversity (GLM: $F_{4,81}$ = 0.49; $p > .05$) or the latency to the first exploration bout (GLM: $F_{4,81}$ = 2.05; $p > .05$; Table 6.5). However, it did have a significant effect on the mean time spent exploring the object, as shown in Figure 6.3.7 (GLM: $F_{4,81}$ = 34.03; $p < .001$). A series of post-hoc tests revealed there were significant differences between each of the object types (Tukey: all $p < .05$), except for between the balanced simple asymmetric object and the unbalanced symmetric object (Tukey: $p > .05$). The exploratory duration for each object was as follows (from longest to shortest): unbalanced symmetric and balanced simple

Table 6.5 – A summary table outlining the three GLM models for the effect of object symmetry and balance (i.e. object type) within a trial on: time (minutes) spent exploring the object; behavioural diversity (number of different exploratory behaviours); and latency (seconds) to first exploration bout in Experiment 4. Sex, origin (10 levels, either breeder or cage ID), home cage number (1–7) and trial order (3 levels) were included in the models as fixed factors, while age was included as a covariate. The object type (balanced symmetric, unbalanced symmetric, balanced simple asymmetric, unbalanced simple asymmetric and unbalanced complex asymmetric) was a fixed factor in all three models.

	Factor	**d.f.**	***F***	***p***
exploration duration	**Object type**	**4**	**34.03**	**< .001**
	Sex	1	1.92	0.170
	Origin	9	1.50	0.164
	Cage no.	6	1.86	0.098
	Trial order	2	0.47	0.629
	Age	1	0.04	0.840
no. different exploratory behaviours	Object type	4	0.49	0.741
	Sex	1	0.00	0.948
	Origin	9	0.56	0.826
	Cage no.	6	0.62	0.717
	Trial order	2	0.59	0.557
	Age	1	0.30	0.586
latency to first exploration bout	Object type	4	2.05	0.095
	Sex	1	0.17	0.681
	Origin	9	1.31	0.242
	Cage no.	6	1.12	0.360
	Trial order	2	0.54	0.587
	Age	1	2.79	0.098

Significant variables are indicated in bold; $n = 105$ for all measurements.

asymmetric; unbalanced complex asymmetric; unbalanced simple asymmetric; and, lastly, balanced symmetric.

6.3.5 Experiment 5: compliance over time

Over all of the days, the time spent exploring stayed approximately the same at approximately 63% (± 17%) of the trial time (GLM: $F_{4,84} = 2.21$; $p > .05$;

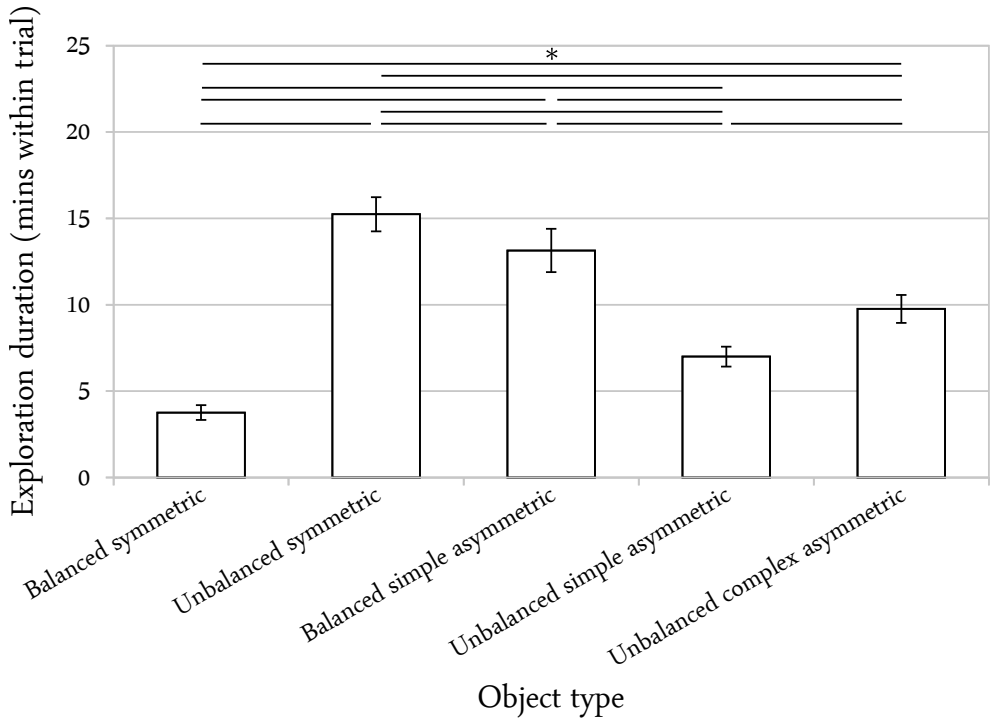


Figure 6.3.7 – A bar chart illustrating the effect of object symmetry and balance on the time spent exploring a target object within a trial in Experiment 4. These two object properties were manipulated in six test objects presented in consecutive trials (shown in Figure 6.2.5). Each object's colour and mass was the same. Balance (or the point of centre-of-gravity) was controlled by embedding weights either in an extreme end of the object, or in its geometric centre. To control for the possible effect of shape complexity on exploration, as opposed to the possible balance effect, two of the asymmetric objects were either simply or complexly shaped. This figure caption corresponds to Figure 6.3.2.

Table 6.6). No significant effect of cube compliance was found for behavioural diversity either across days (GLM: $F_{4,484} = 0.70$; $p > .05$) or within each day (GLM: cube*day, $F_{16,484} = 1.22$; $p > .05$). However, across all five days, there was a significant effect of cube compliance level on the proportion of time spent exploring each cube (GLM: $F_{4,484} = 3.68$; $p < .01$). There no significant effect of day number on this same data (GLM: $F_{4,484} = 0.61$; $p > .05$), but there was a significant interaction found between the cube compliance level and day number (GLM: $F_{16,484} = 81.30$; $p < .001$).

Table 6.6 – A summary table outlining the three GLM models for the effects of cube compliance and day number on: the overall proportion of trial time spent exploring; the mean proportion of exploration time; and the mean behavioural diversity (number of different exploratory behaviour) in Experiment 5. These means were for each day with each cube and were calculated from the 21 kakariki's trials. The proportional time data was arcsine-squareroot transformed. Sex, origin (10 levels, either breeder or cage ID), and home cage number (1–7) were included in the models as fixed factors. Day number (1–5) was a fixed factor in all three models, while cube compliance (levels 1–5) was included as another fixed factor, but only in the last two models.

	Factor	**d.f.**	***F***	***p***
overall % trial time exploring$^{\diamondsuit}$	Day no.	4	2.21	0.075
	Sex	1	0.35	0.553
	Origin	9	1.27	0.265
	Cage no.	6	0.34	0.914
% exploration time$^{\sun}$	**Cube compliance**	**4**	**3.68**	**0.006**
	Day no.	4	0.61	0.656
	Cube compliance × Day no.	**16**	**81.30**	**< .001**
	Sex	1	0.00	0.950
	Origin	9	0.08	1.000
	Cage no.	6	0.02	1.000
no. different exploratory behaviours$^{\sun}$	Cube compliance	4	0.70	0.593
	Day no.	4	1.02	0.397
	Cube compliance × Day no.	16	1.22	0.247
	Sex	1	0.65	0.421
	Origin	9	0.83	0.588
	Cage no.	6	0.51	0.802

Significant variables are indicated in bold. $^{\diamondsuit}n = 105$ $^{\sun}n = 525$

A series of post-hoc Tukey tests revealed the pattern of this effect changed within each trial, as illustrated in Figure 6.3.8. On the first day, the most rigid cube (level 1; Tukey: all $p < .01$) and the most compliant cube (level 5; Tukey: all $p < .01$) were explored for a significantly greater proportion of the exploration time than the cubes of intermediate levels of compliance (levels 2, 3 and 4). This same pattern was found in the second trial, though to a lesser

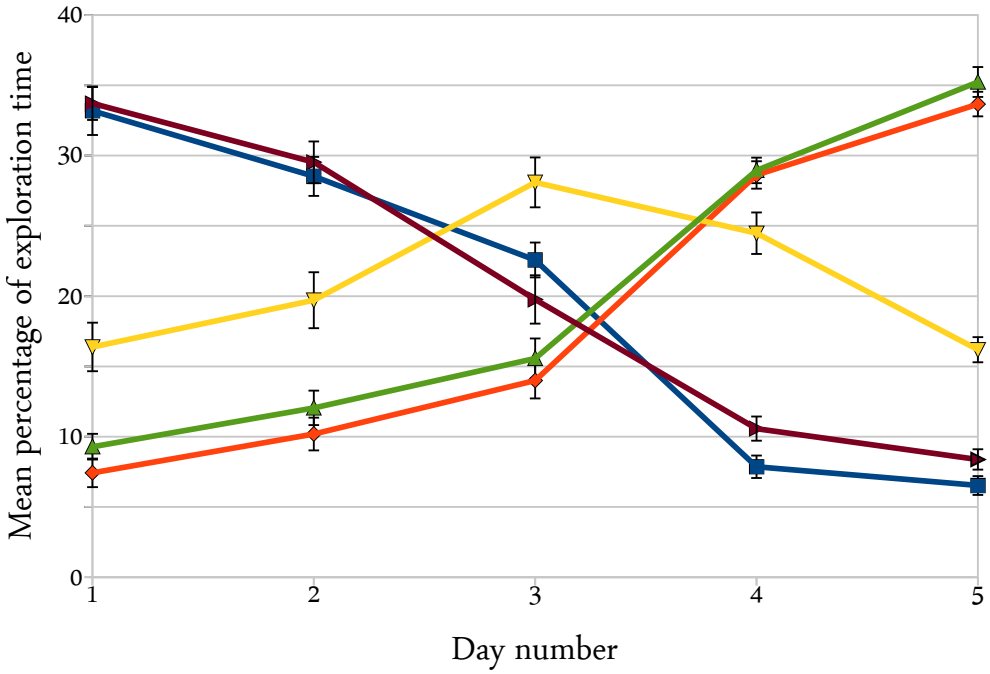


Figure 6.3.8 – A line graph showing the mean percentage of exploration time within a trial spent exploring five cubes of different levels of compliance over five consecutive days in Experiment 5. The cubes were presented to the kakariki simultaneously in a line and are shown in Figure 6.2.6. Each cube's position in the line was randomised in each trial. They were all blue and of the same size, but to create different compliance levels, they were made out of different materials. The most rigid cube (level 1; blue line) was made of plastic, and the next most compliant was made of felt, but filled with sand (level 2; red line). Level 3 was a hard sponge (yellow line), and level 4 was a soft sponge (green line). The most compliant cube (level 5; purple line) was made out of felt, but with little stuffing, so it could be compressed very easily. This figure caption corresponds to Figure 6.3.4.

extent.

In trial 3, it was the most intermediate cube (level 3) that was explored for a significantly greater proportion of time than all the other cubes (Tukey: all $p < .01$), although no significant differences were found between each of the other cubes (Tukey: all $p > .05$). In trial 4, all of the intermediate cubes were explored for a significantly greater proportion of time than both the most compliant and the most rigid cubes (Tukey: all $p < .01$). In the last trial, this

was again true for level 2 and level 4 (Tukey: all $p < .01$), but not for level 3, which was now explored for approximately the same proportion of time as the level 1 and level 5 cubes (Tukey: all $p > .05$). Thus, now level 2 and level 4 was explored for a significantly greater proportion of time than level 3 too (Tukey: both $p < .01$).

6.4 Discussion

These experiments demonstrate kakariki exploration is not random, but relatively structured, selective and sensitive to particular features and salient properties of their surrounding environment. Through a series of simple behavioural tests with simple objects, we have shown how exploration is influenced by the different edges/parts of a target object, its shape complexity and novelty. Visible cues (e.g. colour, shape or symmetry) are important, but invisible, functional cues (e.g. centre-of-gravity/balance) play a greater role in directing exploratory behaviour. Moreover, unexpected changes in the object (those not predicted by the visual appearance) focusses exploration.

6.4.1 Surface transitions

More exploratory behaviours were performed upon the corners and indents of objects over areas of high curvature, which were in turn explored more than flat surfaces. However, against our hypotheses, this was not reflected in the diversity of exploratory behaviours performed on these different object parts. This may be because each of these surface transitions provide different types of information about the possible properties or affordances of an object.

Lockman (2000) emphasised how sufficiently cognitively-developed humans place flat edges of a cornered object on flat surfaces for stability, while

they push round objects on continuous surfaces to see if they roll. The corners and indents of objects are particularly prominent, cueing the key points along its geometry (Bushnell and Boudreau, 1993; Spelke et al., 2010; Lee and Spelke, 2011). They can prime visual and haptic information about how best to interact with the object category (Taylor and Zwaan, 2010). Corners provide optimal points for grip, allowing for more complex exploratory manipulations (e.g. Bryant et al., 1972; Wing and Lederman, 2009). Once the corners have been visually identified, it is efficient for the animal to target these object parts first, especially if time is limited. Then, according to the initial haptic information gained from the object's edges, the animal could vary their subsequent exploratory actions to gather further information about its affordances (e.g. see robotic analogy in Charusta et al., 2009).

Next, areas of high curvature were explored by the kakariki. These provide further information about an object's geometry and cues, such as about whether it can roll. This is interesting in considering an artificial intelligence finding: Ravishankar et al. (2008) found it is easier to design an artificial agent that recognises deformed objects by placing representational emphasis on the bending around points of high curvature.

While little work has been done on how animals perceive the affordances of curves, there has been work on how animals recognise differently curved surfaces (Williams, 1978; Tomonaga, 1998; Norman et al., 2004; Brooks and Wasserman, 2010; Cook et al., 2012). For instance, Cook et al. (2012) described how pigeons (*Columba livia*) visually perceive object shapes by focussing on convex and concave curved surfaces. Pigeons readily discriminated and generalised to novel perspectives, dynamic changes in shading and to novel

three-dimensional shapes. Note that this discrimination was performed using purely visual information, and that pigeons are not particularly adept at discriminating between different textural cues, whereas parrots seem to be (Brooks and Wasserman, 2010).

The smooth, flat surfaces of the objects were unlikely to provide as much information as corners and areas of high curvature, so the kakariki spent fewer exploratory resources on them. Perhaps, if these surfaces had a rough texture, the kakariki would have explored them more, but this needs verification. Texture can provide information on properties such as friction or compliance (Adolph et al., 2010; Brooks and Wasserman, 2010). Human infants selectively explore textured objects after 18 months of age (Molina and Jouen, 1998), when sufficient cognitive representation has developed for attributing specific meaning to different object categories (Belsky and Most, 1981; Bushnell and Boudreau, 1993).

From a more general perspective, edges are important for a range of animals when navigating around the environment and for detecting different objects (e.g. Cook, 2000; Spelke et al., 2010; Soto and Wasserman, 2012; Cook et al., 2012). Edge cues (e.g. through contrasting surfaces) are particularly important for budgerigars when visually detecting different environment features in the surrounding scene, particularly in guiding landings (Bhagavatula et al., 2009). This is often in preference to other visual cues like colour. Budgerigars are well-known tetrachromats*, which suggests this adaptation predates the evolution of colour vision, or that colour is not a reliable cue to use in these circumstances. As a visually contrasting edge is likely to be an object, it would offer psittacine feet a good place to grip (Gibson, 1950).

Edges are not only prominent cues for the visual system, but also the haptic system. Exploring 1-year-old infants display many contour-following manipulations (Lederman and Klatzky, 1987). The authors argued, of the many other exploratory manipulations studied, this was the only one providing useful information about objects' configurational shapes*. Surface transitions also haptically cue different object relations*; later important for problem-solving and tool-use (Bourgeois et al., 2005).

Clearly a combination of cues is important. As Parron and Washburn (2010) showed with macaques (*Macaca mulatta*), proper object identification only occurs with both edge and surface/texture cues. Future work is needed on how the pattern/sequence of exploratory behaviours may change according to what cues are perceived by different surface transitions. It would be interesting to see how this may change over trial time, with a similar design perhaps to Experiment 5 (subsection 6.2.8). Renner and Seltzer (1994) conducted sequential analyses of rat object exploration, across a range of behaviours. They found exploration patterns varied with object characteristics and across individuals.

It is also important to note our analysis was relatively opportunistic and so the objects provided were not designed to have equal numbers of corners, curves and flat surfaces. It is possible our observations are therefore simply the result of the parrots touching over/under-represented features. Another experiment should be designed specifically for object surface transition effects within a single set of conditions. Nonetheless, the very fact this result was consistent across a range of object types and over a longer period of time highlights its robustness.

6.4.2 Shape complexity

As hypothesised, as the shape of an object becomes more complex (i.e. has a greater number of faces), the kakariki spent longer exploring it, performed a wider diversity of behaviours upon it, and took longer to approach the target object. With regards to the last finding, the kakariki may have taken longer to approach the target object when it was complex, as with the garden warbler, because complex objects are more likely to hide threats (e.g. Greenberg, 1983; Mettke-Hofmann et al., 2006). The parallel motivation of neophobia* initially dominated the exploratory motivation in the kakariki. Objects with more surfaces, angles or holes are likely to provide more opportunities to hide dangerous substances or a predator (Mettke-Hofmann et al., 2006). Complex objects may also take more time and energy to explore than simple objects, which would impose an added ecological cost to exploring them, in addition to the potential threat they could hide.

Nonetheless, the initial neophobia was clearly replaced by the motivation to gain more information about the novel complex object. The kakariki spent longer exploring as the shape complexity increased, because complex objects likely contain much information previously unknown. Similarly, the kakariki displayed greater behavioural diversity with more complex objects, as they afforded more behaviours to be performed on them. This is supported by studies on chickens (*Gallus gallus*; Jones et al., 1996) and rats (Berlyne, 1950; Zimmermann et al., 2001), which have been shown to spend more time exploring complex objects rather than simple objects. Similarly, a previous study on kakariki found those living in enriched environments performed a wider diversity and more complex behaviours than those in unenriched environments, when exposed to more complex toys (chapter 5).

However, a study on another parrot species (*Amazon amazonica*) showed enhancing physical complexity in a captive environment actually reduces the motivation to explore objects (Meehan and Mench, 2002). This is perhaps because enriched individuals have more experience, so they do not need to explore novel objects as much as unenriched individuals. However, the same authors in another study showed enhanced physical complexity simultaneously reduces stereotypic feather picking and increases foraging behaviour (Meehan et al., 2002). This perhaps supports the reductionist hypothesis: exploration is just a side-effect of the motivation to seek stimulation in the absence of primary drivers like hunger or thirst (e.g. Miller and Dollard, 1941; Harlow et al., 1950).

More research on how shape complexity influences the structure of exploratory behaviour has been conducted in human developmental psychology (Switzky et al., 1979; Frey and Kaiser, 2011; Kawa and Pisula, 2010). In particular, Switzky et al. (1974) found increasing stimulus complexity with random polyhedra produced a longer exploratory time in both 4–7 year-olds (linear function) and 2 year-olds (curvilinear function). This has been supported in other studies, but not as the prime factor investigated (Klatzky et al., 1991; Klatzky and Lederman, 1993; Ruff et al., 1992).

One should bear in mind, however, we do not fully know the background of all of the kakariki. They may have previously experienced other round objects like the sphere in this experiment, or other simple objects in their natural home cage or rearing environment. Therefore, perhaps their increased exploratory response to the objects with more faces is just a response to novelty. It is common finding that individuals explore more with novel objects

than familiar objects. This presents scope for further work, but our strength of results – i.e. the highly significant linear trend across six shapes and three exploration measures – nonetheless presents some interesting implications for the field.

6.4.3 Visible cues and centre-of-gravity

As hypothesised, the kakariki initially spent a greater proportion of the exploratory time focussed on the novel red ball, rather than the familiar piece of rope, but this effect decayed with time. Their overall exploratory level (whether exploring ball or rope) decreased over the four days in this first experimental phase. In the second phase, the kakariki explored an invisible centre-of-gravity change in the ball for longer than a visible change (i.e. colour or shape). All of the object property changes resulted in longer exploration than the control condition, where no change occurred.

There was also a behavioural diversity effect, but, contrary to our hypotheses, this did not follow the same pattern of effects as the exploration duration. Only a shape or centre-of-gravity change induced a wider variety of exploratory behaviours than the control. Nonetheless, as predicted, the visible changes had an impact on the latency to the first exploration bout.

Let us first consider why kakariki exploration was initially greater with the novel object than the familiar object, but repeated exposure to both objects decreased this exploratory level over time. Over the last 50 years or so, in a range of contexts and in a range of other species, novelty has been shown to increase exploration (for a review see Wood-Gush and Vestergaard, 1991; Heyser and Chemero, 2012). It is one of the few well-established, systematic

findings about exploration patterns in humans and non-human animals (e.g. Berlyne, 1960; Henderson and Moore, 1980). It is thought to be due to an individual's recognition memory*: the novel object is preferentially explored, as it diverges from what the individual remembers. Inglis and colleagues (e.g. 2001) have argued the animal is motivated to behave in this way by the need to find out more about the unknown, especially when within an unpredictable, variable environment. Schulz and Bonawitz (2007) and Cook et al. (2011) have shown children's exploration is structured to gather more information about ambiguous or confounded evidence.

By the time the kakariki were exposed to one of the four experimental changes in the object property (visible/invisible) on the fourth day of this experiment, there was no significant difference in the exploration time spent on the familiar piece of rope and the once novel red ball. In other words, there was no difference in exploration between the last day of the first experimental phase and the control condition day of the second experimental phase (Figure 6.3.4). Perhaps the difference in exploratory response to one of the object property changes was due to this prevalent novelty effect. However, this does not necessarily explain the relative difference in responses to each of the types of object property changes. Not all aspects of novelty (induced by object property changes) may be equally salient to the kakariki.

Experiment 3 has demonstrated visible cues are clearly important to kakariki. In particular we can see this in our latency results: the kakariki were slower to approach the target object when there was a visible change in colour. However, effects were stronger when the visual cues have more functional implications, as for instance, the kakariki were even slower to approach when there

was a change in shape. These latency results are consistent with our other findings discussed in subsection 6.4.2. Colour is less likely to have an effect on how an object behaves when acted upon, whereas shape does. In this case, the red cube when pushed could no longer roll like the red ball. The study by Heyser and Chemero (2012) on mouse exploration highlighted the relative importance of choosing test objects based on their functional cues, rather than just their visible cues. The authors also noted the importance of an individual's abilities, as different individuals will often perceive different affordances of the same object within the same physical space. Likewise between species, a branch, for instance, can have perch affordances for birds, but tool-use affordances for primates.

Greater exploration occurred when a property change occurs invisibly, especially when it affects how an object 'normally' behaves – when it goes against an individual's expectations of how the world works. The ball-bearing inside the red hollowed-out ball did just this: the centre-of-gravity moved with the ball-bearing, rather than the ball itself, so the ball rolled around in an unusual manner (see also discussion of our other results on balance in subsection 6.4.4 below). In other words, the ball's movement deviated from what was known, thus eliciting more exploration – more information was needed about these unpredictable movements.

Perone et al. (2008) found children attended more to changes in an action (i.e. a functional change) on an object than changes in the appearance of an object. Furthermore, Schulz et al. (2008) showed children's exploration was more directed at changes within an object category (i.e. against expectations), than changes between object categories, and even less so for

arbitrary/aesthetic changes. We would like to suggest in our experiment, the kakariki were more sensitive to the centre-of-gravity changes within the 'ball category', although the presence of the new 'cube category' also stimulated their curiosity.

Centre-of-gravity has been shown to be an important perceptual cue in exploration for humans and for non-human animals, perhaps because it is a particularly salient cue for an object's properties across various object types (Bushnell and Boudreau, 1993; Wing and Lederman, 1998; Pare and Dugas, 1999; Zhu and Bingham, 2010). Under a range of experimental conditions, great apes have displayed greater cognitive performance when problems are grounded in causal relations with centre-of-gravity information, rather than arbitrary relations with colour information (Regia-Corte et al., 2012; Schrauf and Call, 2010; Hanus and Call, 2008, 2011). Several researchers have speculated about whether such centre-of-gravity perception, used for drawing causal inferences* and problem-solving, is the precursor for more abstract reasoning for concepts like gravity and support (Hood, 1995; Hanus and Call, 2008; Cacchione and Krist, 2004; Cacchione and Call, 2010).

Capuchins (Caebidae) are well-known extractive foragers: a wide range of field studies have shown how they have excellent centre-of-gravity perception and exploratory abilities enabling them to choose appropriately-embedded food items, and even appropriately-weighted tools to crack open particular food items (Ferreira et al., 2010; Visalberghi and Neel, 2003). Although centre-of-gravity perception has not been studied extensively in non-primate species, a range of animals has been shown to be able to make causal inferences (e.g. Aust et al., 2008). It stands to reason that extractive foragers other

than capuchins (e.g. parrots) use centre-of-gravity to make causal inferences about the world around them. We believe these results show kakariki are one such species. Some very recent studies suggest the Mexican jay (*Aphelocoma ultramarina*) may be another such species (Lee et al.; Fuszara et al., in prep.).

An alternative explanation for how the kakariki explored the ball with the ball-bearing in it more than the other objects is that they were just responding to auditory cues. The ball-bearing inside the hollowed-out ball did make a small rattling noise when moved. In the future, perhaps an easy control for this issue would be to play background white noise in all the conditions. This is a common technique in laboratory behavioural tests and, once habituated for a short time, does not cause the animal any stress or distraction from the task at hand (e.g. in Brydges et al., 2011).

Another issue with our method was that we cannot completely disentangle the object properties (colour, shape, centre-of-gravity) in the second phase of the experiment from object novelty (rope, ball) in the first experimental phase. This is because novelty increases with deviation from the original red ball. For instance, the shape change (cube) could be argued to be more novel than the colour change (blue). The second phase also investigated object novelty. Additionally, in the first phase, the ball may simply have been more attractive than the rope, which resulted in more exploration. If this experiment were to be repeated, it would be better for the first phase to have two groups of kakariki: one group familiar with the rope and one group familiar with the ball.

6.4.4 Symmetry and balance

In agreement with our hypotheses, the kakariki explored for longer when the centre-of-gravity was in an unexpected location according to its symmetry. In other words, the most exploration occurred when a symmetric object was unbalanced (centre-of-gravity to one side), or an asymmetric object was balanced. When the centre-of-gravity was in accordance with the visual symmetry cues, the (unbalanced) asymmetric objects were explored for longer than the (balanced) symmetric object. Lastly, the unbalanced complex asymmetric object was explored more than the unbalanced simple asymmetric object. However, contrary to our predictions, this pattern of results was not reflected in the behavioural diversity. Additionally, no effect for latency to the first exploration bout was found, although a significant difference was anticipated between the complex asymmetric object and the simple asymmetric object.

When the centre-of-gravity was where it was expected, the kakariki explored an asymmetric shape more than a symmetric shape. This may be due to its unusual irregularity, thus being relatively novel compared to what they have previously experienced (see the early discussion on object novelty in subsection 6.4.3). On the other hand, symmetric objects are quite predictable in shape, so not as much information can be gained from them, so not so many exploratory resources need to be spent on them.

However, when the centre-of-gravity was not where it was expected, the time spent exploring the object increased even further. There was no significant difference between the time spent exploring the balanced asymmetric object and the unbalanced symmetric object. These results can be explained

by much of our discussion above in subsection 6.4.3. It is interesting to note this result is consistent, even with the slight methods change with no prior habituation phase (subsection 6.2.6 and subsection 6.2.7). So whether an object is symmetric or not, symmetry does seem to be an important visible cue for gaining information about it. If an object is symmetric, then the centre-of-gravity is expected to be in the approximate geometrical centre of the object. When this is not the case, the kakariki are motivated to explore more to find out why this might be.

Children with different knowledge of how objects balance display different exploratory behaviour patterns on asymmetric objects with different centres-of-gravity (Bonawitz et al., 2012b). In the adult literature, Zhang et al. (2010) presented participants with asymmetric objects with the centre-of-gravity in different locations and measured their anticipatory grip forces. They showed how the planning of object manipulations compensating for unexpected changes in balance was reliant on sensorimotor memory formation and retrieval in two separate object property domains: kinematics and kinetics*. Others have shown when an object's centre-of-gravity is located away from the grip axis, grip force and object exploration is modulated by dynamically anticipating object torque (Wing and Lederman, 1998; Crevecoeur et al., 2011).

Perhaps the kakariki are testing and refining their hypotheses about the world by exploring and acting on it (Demery et al., 2010; Arriola-Rios et al., 2013). Rats alter the speed and pattern of their whisking behaviour when they encounter unexpected shapes and textures along object surfaces (Pearson et al., 2007; Grant et al., 2009). Is this an implicit, sensorimotor response

to novel surfaces, or is the rat seeking an explanation to unexpected properties?

Povinelli and Dunphy-Lelii (2001) argued they found evidence for this 'explanatory drive' – as a subsystem of the exploratory drive – in children, but not in chimpanzees. When faced with an oblong block that, contrary to previous experiences, would not stand up (it had slightly bevelled edges), the chimpanzees failed to explore it to diagnose the cause, whereas the children did. The authors believed while some non-human primates have an intrinsic interest in functional and perceptual properties of objects, only humans have an intrinsic motivation to discover why objects have the properties that are apparent to the senses (see also Gopnik, 2000). However, just because the chimpanzees may not have been explicitly seeking explanations, that does not mean they were not still passively finding explanations (Dutant et al., 2004) – the same reasoning could apply to our findings about kakariki.

Shape complexity as a cue did have some influence on exploration, as well as balance and symmetry, because the complex asymmetric object was explored more than the simple asymmetric object. This is explained by our discussion in subsection 6.4.2. The lack of a significant difference between the latency to the first exploratory bout for the complex and the simple asymmetric objects is interesting, considering our other findings about shape complexity (subsection 6.4.2). Perhaps this is because, for the kakariki, balance is a more important cue to explore than shape complexity – invisible cues are attended to more than visible cues. This explanation makes sense when compared to our other results in Experiment 3, where greatest exploration occurred when an object had an invisible change in its centre-of-gravity, rather

than when there was a visible shape or colour change (subsection 6.4.3). Alternatively, perhaps the difference in exploration between the simple and complex asymmetric objects is simply because, the complexity between the objects was not great enough to produce a positive result.

Note there was also no overall effect of object type on latency to first exploration bout, including between all of the simple objects. Even though the visible change between the symmetric and simple asymmetric objects does introduce some novelty, the dumb-bell shape of the objects only changed slightly, which may explain this lack of difference in approach latency. Clearly, the invisible balance cues could not influence the approach latencies, as such cues would only be revealed once the animal had started haptic exploration. It is not clear in our last finding, however, why the object type had no effect on behavioural diversity, unlike in Experiments 2 and 3 (discussed in subsection 6.4.2 and subsection 6.4.3).

6.4.5 Compliance over time

As hypothesised, the kakariki initially started exploring the most compliant and the most rigid objects, but over the following days, they spent progressively more time exploring the intermediate objects. In other words, the kakariki next focussed their exploration on the cube of middle compliance (level 3), then turned their exploratory focus on the cubes of the next levels of compliance; the second-most compliant and the second-most rigid cubes. There was no effect of behavioural diversity in this experiment though, as to be expected. The overall amount of time spent exploring stayed approximately the same across trials as well. This suggests the kakariki had a preferred level of exploration for investigating compliance, and they just allocated the

time spent among the different cubes according to their interest in the different levels of compliance, which is perhaps dependent on experience. Note this is in contrast to the overall exploration level in Experiment 3, which decreased over time; perhaps because there were only two objects present, one of which was very familiar (subsection 6.4.3).

These results suggests kakariki have some sort of exploratory strategy. Our findings are consistent with the idea that animals first collect information about the most extreme categories/examples of a particular object property – in this case compliance (Demery et al., 2010). The extreme examples would provide general information about the boundaries of different categories (e.g. rigid versus compliant) quickly, likely allowing efficient energetic use. Then exploring animals are thought to gradually refine their knowledge about that property, by focussing their exploration progressively more on the intermediate examples (Arriola-Rios et al., 2013). This would be an adaptive mechanism particularly for animals living in unpredictable, variable environments. As long as there was little risk from other sources (e.g. predators), they could gain as much information about the unknown as possible (Inglis, 1983).

This strategy is likely combined with some sort of object categorisation mechanism (e.g. as in Klatzky and Lederman, 1993). Categorisation greatly reduces the computational complexity of perceiving objects and their affordances and has been shown to occur in a range of animals (e.g. Shutts et al., 2009; Crouzet and Serre, 2011; Xu, 2011; Soto and Wasserman, 2012; Wasserman et al., 2012). From the earlier experiments discussed in subsection 6.4.3 and subsection 6.4.4, we can see the kakariki seem to have certain expectations about different object categories, and when these expectations are viol-

ated, they seem to explore more to refine their knowledge about these categories. Perhaps the object category being formed in this experiment was the 'compliance category'.

This particular experiment was only carried out over five days, but perhaps this strategy of refining knowledge over time reflects a more general strategy, where information is continually gathered to continually extend knowledge throughout one's life (Chappell et al., 2012). Exploration has been shown to be prevalent throughout parrots' lives, as with other species living in variable environments (Gibson, 1988; Bekoff and Byers, 1998; Luescher, 2006). This continual state of learning may enable the information to be represented in the animal's brain in a hierarchical structure (Arriola-Rios et al., 2013). The simple categories of information could be combined to form an overarching categorisation layer (e.g. Karmiloff-Smith, 1995; Chappell and Sloman, 2007; Arriola-Rios and Savage, 2007). As yet though, there has been no direct experimental evidence for a hierarchical representation that is continually refined with time.

Inevitably, exploring a compliant object visually results in the distortion of its edges (Teschner et al., 2004; Arriola-Rios et al., 2013), which are known to further contribute to the formation of object categories (see also discussion in subsection 6.4.1). This principle has been applied in a working robotic hand, where grip was adapted to the level of compliance, object type and material visually perceived (Cretu et al., 2012). Human infants are known to be able to gather information about compliance at 1 month of age from coordinated mouth and hand exploratory actions (Gibson and Walker, 1984). Rochat (1987) showed the patterns of these actions, as with the kakariki, be-

came gradually more targeted with time depending on the level of compliance. Older infants likewise gather information about surface compliance in a selective manner through locomotory exploration once they learn to crawl and walk (Gibson et al., 1987; Bourgeois et al., 2005).

There is little work on compliance exploration in the non-human animal literature. Recent work has recognised how compliance is an important property for arboreal birds and primates moving around the canopy (e.g. Bonser, 1999; Thorpe et al., 2007a). A good level of physical understanding* is particularly needed for heavy species like orang-utans and compliance has been associated with complex cognitive capacities like planning (Tecwyn et al., 2012).

One study has described how capuchins (*Cebus apella*) were consistently able to select novel tools appropriately based on their compliance, across a range of laboratory-based tasks (Manrique et al., 2011). While compliance was the most important cue in this study, the tools the capuchins used also varied in colour, diameter and material. This is encouraging, because one possible limit of our experiment was the cubes presented to the kakariki, while all differing in the level of compliance, also sometimes differed in the material they were made out of. Compliance as a property is intrinsically related to the material/texture of the object. This is illustrated by the simple fact it is difficult to source a compliant plastic cube, as it is difficult to source a rigid sponge cube. The developmental psychology literature often describe children's exploration of compliant objects in the same breath as their exploration of textured objects, or sometimes even interchangeably (reviewed in Bushnell and Boudreau, 1993).

6.4.6 Summary

By observing exploratory behaviour, we can gain an insight into how different animals gather information and learn about the world around them. We have shown how novel, functional or unexpected environmental changes seem to result in increases in exploration. We have highlighted some environmental factors that may be important to determining the pattern of exploration, at least in kakariki. From here, we can start to reason about what some of the underlying representational or learning mechanisms may be.

For instance, as kakariki live in such variable environments, they are likely born with a quite a flexible learning framework, which is supported by sensory predispositions to particular environmental stimuli and a series of targeted exploratory behaviour strategies (e.g. to particularly compliant branches or weight of embedded food items; Chappell et al., 2012). They may also have some innate 'core knowledge' of physical properties, like gravity, solidity, connectedness, continuity and balance (like those described in Spelke, 2000). These structured exploration strategies likely allows a kakariki to gain information more efficiently, but it needs to balance the amount of useful, relevant information obtained from its environment against the energy expended in gaining it (Chappell and Sloman, 2007).

In the past, we have proposed a general 'Three-stage Theory of Exploration' for how different animals may gather different kinds of information throughout their lives (Demery et al., 2010; Arriola-Rios et al., 2013). As an exploring animal learns about how the world works, it progresses through three stages to form a particular theory, such as about how a branch bends. These stages are: the forming; the testing; and the refining of hypotheses.

Each hypothesis is specific to a particular group of environmental processes or object affordances ('exploration domain'), but they may also overlap and be generalisable in novel situations. As the animal progresses from one stage to the next, it uses a combination of increasingly complex learning mechanisms, depending upon the environmental problem it is faced with. However, the details (e.g. time-scale in hypothesis development) are likely to vary between different species, individuals, exploration domains and environmental situations. Indeed a species may not progress all the way to the final stage, where simple, yet sophisticated, learning mechanisms (e.g. probabilistic learning and trial-and-error), supported by certain sensorimotor predispositions may suffice.

We would like to tentatively suggest the results reported in the chapter are evidence that kakariki display at least the characteristics of the first stage of our theory (e.g. trial-and-error and sensory predispositions), and some of the features of the second stage (e.g. perform certain actions in certain contexts as in the compliance experiment). It is currently not clear from our results whether kakariki have other elements of the second stage, such as sensitivity to physical rules. There is certainly no evidence yet of final stage in kakariki, such as the ability to generalise flexibly to similar but novel situations.

Our results further do not clearly show how the kakariki may change the exploratory behaviours according to the different cues they perceive, or what the specific pattern of their exploration is. It would also be interesting to look at age and experience effects on the exploration strategy used. Moreover, all of our experimental data was recorded by a single observer, although videos

were utilised – inter-observer reliability still needs to be determined.

In the next chapter (chapter 7), we would like to investigate another species that lives in a variable environment: humans. Like kakariki, humans have adapted by developing flexible cognitive capacities, manipulatory dexterity and a highly exploratory nature (Buchsbaum et al., 2012). However, an advantage of studying humans over kakariki is that through language, we can more easily communicate the goal of the task, which reduces habituation and training time..

CHAPTER 7

Exploratory learning strategies in human children

Material from of this chapter has formed part of three publications (Demery et al., 2010; Chappell et al., 2012; Arriola-Rios et al., 2013).

Piaget's view that children learn through exploration is widely accepted as being integral to cognitive development. Surprisingly few scientists, however, have systematically investigated how exploration is structured to support learning mechanisms in different situations. We presented a series of three tasks involving novel objects and physical problems to children (aged 4 to 7 years) to examine in detail the process of exploration in different contexts. We found that children pay more exploratory attention when there are invisible, more functional changes (e.g. weight) over visible, less functional changes (e.g. colour) in an object. Children understand how simple physical principles govern the behaviour of objects, but here we discuss to what level this extends across development depending on the exploration strategy employed. Further, we consider how children utilise exploration to gather information about hidden items. We hope these findings this will give us insight into how humans and other animals process information in a wide range of environmental situations.

7.1 Introduction

ONE of the most widely accepted views in human psychology is that exploration is integral to a child's learning and causal understanding* about the world around them. It is thought, from birth, the child's visual

and haptic systems are primed for gathering information (Gibson, 1962, 1988; Turvey, 1996; Rochat, 2001). Through active interaction and play with different objects, children 'construct knowledge'* about how things work around them and store them in some kind of internal representation* (Piaget, 1929, 1952; Spelke, 2000; Karmiloff-Smith, 1995).

Surprisingly few scientists, however, have systematically investigated how exploration is structured to support learning mechanisms and even fewer have studied it outside a human cognitive development context (Schulz et al., 2008). Indeed, there is much evidence that children, and even adults, are poor at explicitly designing their own experiments to gather causal information (Amsel and Brock, 1996; Masnick, 2002; Kuhn and Dean Jr, 2004; Zimmerman, 2007). This has led some to point towards a more intrinsic motivational account (White, 1959; Hunt, 1965), which says exploratory behaviour does not have inherent structure, and it may be a byproduct of some other more important biological function (e.g. foraging; Miller and Dollard, 1941; Harlow et al., 1950). If this were true though, how does a child process all of the vast 'buzzing, blooming confusion' (James, 1890, page 462) received through their senses, to eventually be able to reason abstractedly* about the world in the coherent and sophisticated manner that we know we can do as adults (Gopnik and Wellman, 2012)?

Experiments conducted with older participants (aged 10 years and above) has involved several measures (e.g. visual, verbal or manipulatory; Henderson, 1988; Gaver, 1996). These studies have illuminated how exploration probably has no single underlying representation, but is made up of interconnected, but distinct domains (also see Karmiloff-Smith, 1995). Each of these

'exploration domains'* are specific to a particular group of object affordances (i.e. action possibilities) or environmental processes (Chappell et al., 2012; Arriola-Rios et al., 2013). For instance, Vandenberg (1984) ran correlational analyses on the individual differences in exploratory style, or preferences for specific object features (e.g. novelty versus complexity). He found little correlation between 12-year-olds' preferences for object complexity and novelty; or between the attention paid to different objects and the detail of the actions performed on them.. Nonetheless, the adult exploration literature consistently shows how exploration in infancy leads to greater information gain, which is linked to greater problem-solving abilities in adulthood (e.g. McReynolds et al., 1961; Goodnow, 1969; Caruso, 1993). Therefore, it is important to investigate how these different domains may interact early on in life to support causal learning.

Traditionally, qualitative, rather than quantitative, methods have been employed to study exploration in young children (Schulz, 2012; Power, 2000). In recent years, this trend has somewhat changed, where researchers have concentrated on what *simple* object characteristics direct children's exploration (e.g. Gibson and Walker, 1984; Baldwin et al., 1993; Ruff and Capozzoli, 2003; Oakes et al., 2012). These have revealed, on top of the well-established object novelty effects (e.g. Berlyne, 1960; Henderson and Moore, 1980), infants spend longer exploring when objects are complex (e.g. Switzky et al., 1974), physically responsive in some way (e.g. McCall, 2011; Rosenberg and Butler, 1982), or have distinctive textures (e.g. Bushnell and Boudreau, 1993; Molina and Jouen, 1998). These early behaviours may reflect how the individual is beginning to gather information and form representations about the world around them (Demery et al., 2010). They may be able to detect

patterns in their environment using simple learning mechanisms, such as by trial-and-error (Arriola-Rios et al., 2013).

A few studies have also started to looked at how simple exploration is targeted to particular situations. Children seem to target specific exploratory actions at specific object properties, such as following contours to extract information about shape, or pressing down on an object's centre to gather information about compliance (Lederman and Klatzky, 1987, 1993). The type of information being gathered can be estimated by observing how various actions are expressed, such as how different objects are wielded to gather information about weight and balance (Turvey, 1996; Turvey and Carello, 2011). This may reflect a later stage of cognitive development, where the infant is testing its knowledge* about the world by acting on it in a directed way, rather than simply repeating the same actions regardless of the circumstances (Demery et al., 2010; Arriola-Rios et al., 2013). In other words, even in infancy, individuals seem to be gradually learning what kinds of actions are most effective in each situation (Chappell et al., 2012).

Other developmental psychologists has looked at the other end of the spectrum; when *complex* cognitive capacities have already fully developed, such as being able to understand different object relations* and make causal inferences* (Rochat, 2001; Gopnik and Schulz, 2007). Spelke (2000) argued all infants are born with innate rules about the physics of the world, such as cohesiveness, continuity and solidity. In other words, objects maintain their geometric shape as they move, trace continuous paths both in time and space, and no two objects can exist in the same space at the same time. Researchers investigating each of these 'core concepts' typically utilise the ex-

pectancy violation technique, by presenting children of different ages with impossible causal events. Then they measure their relative looking times, or search behaviour (e.g. Baillargeon, 2002; Mash et al., 2003; Hood et al., 2006). Knowledge about other object properties seems to be learned with time (Sloman, 2009). Although no one has explicitly measured it yet, these innate rules may further help an individual to direct exploration appropriately in specific situations (Demery et al., 2010). These experiences would likely extend and refine an individual's knowledge about the world (Chappell et al., 2012; Arriola-Rios et al., 2013).

Some researchers view children as 'young scientists with intuitive theories' about the world, able to infer explanations for the causal events they observe (e.g. Siegler and Liebert, 1974; Shultz and Ravinsky, 1977; Sedlak and Kurtz, 1981; Kuhn, 1989). By five years of age, children can verbalise their explanations, but there is evidence of an abstract understanding of causal relations occurs even earlier, in preschoolers (e.g. Das Gupta and Bryant, 1989; Sobel et al., 2004). Gopnik and Meltzoff (1998) contended the human mind is particularly adapted to seek explanations, finding it an intrinsically rewarding experience. Exploration is key to children forming, testing and refining their different hypotheses about the world (Demery et al., 2010). By the time children have progressed to the final stage of refining their hypotheses, they have likely developed more complex learning mechanisms than employed earlier, capable of identifying mistakes and gaps in their knowledge (Chappell et al., 2012; Arriola-Rios et al., 2013).

A few have investigated how exploration is structured to support learning and hypothesis-testing (Legare, 2012). Particularly prominent is a series

of studies conducted by Schulz and colleagues (summarised in Schulz, 2012). For instance, they showed children increase their exploration, and explore more selectively, when faced with ambiguous information. Children also seem to be sensitive to object categories and to discrepancies between what they believe, based on what they have previously experienced, and what they observe.

However, Schulz et al. have explained such behaviour by employing probabilistic models like Bayesian networks* (Glymour, 2003; Gopnik et al., 2004; Tenenbaum et al., 2006). Briefly, they argue individuals represent causal structure through some sort of representation that has a series of interconnected, random 'nodes' (the causal events), where each connection ('edges'; the causal relations) has an associated value. While probably true, we assert there is likely a combination of simple and complex mechanisms at work, depending on the situation the individual faces (Arriola-Rios et al., 2013). For instance, if a monkey were planning a safe, but novel, route through the canopy, they may use some form of trial-and-error learning combined with causal reasoning. Nonetheless, from this review, we can see that:

1. from infancy, exploration in humans seems to be directed at various simple object characteristics;
2. later on in development, exploration is likely aided by more complex capacities like physical rules* and causal inferences.

Thus, in this study, we aim to fill the gap between these two points by measuring exploration in children aged 2–6 years in three distinctive tasks. Unlike previous studies, we are not so much interested in whether children success-

fully complete a task or not, but how exploratory behaviour may aid task completion. Each task is designed to address a different aspect or domain of exploration, specifically:

1. visible and invisible cues;
2. physical rules;
3. causal inferences.

As a secondary aim, we would like to see if exploration duration and diversity changes with age in each exploration domain. By observing the exploratory behaviour of the children before and after different task goals' attainment, we can begin to discuss the possible underlying learning mechanisms being used (Chappell et al., 2012).

Previous work has shown children are sensitive to object category membership, especially in relation to their functional properties, or what actions they afford, rather than any merely aesthetic properties (Lansink et al., 2000; Perone et al., 2008; Oakes et al., 2012). Categorisation has also been shown to be important later for making causal inferences and abstracting concepts* (Welder and Graham, 2001; Nelson, 2004; Davidson and Gelman, 2004). Thus, in our first experiment we ask if subtle changes in invisible functional cues (e.g. action) about object properties are attended to more than changes in non-functional visible cues (e.g. location). Nonetheless, any changes in the environment have been shown to increase exploration (e.g. Berlyne, 1960; Henderson and Moore, 1980). Thus, we predict that:

- when a change in location or action occurs (relative to no change), this

will result in:

  - a longer time to attain the task goal;
  - more exploration (longer exploration time and greater behavioural diversity);

- and the same holds true for an action change relative to a location change.

Since the understanding of how simple physical rules govern the behaviour of objects seems so integral to human cognitive development (Spelke, 2000), we were interested in how children use them to direct their exploration. Many animals (e.g. predators) need to particularly understand the object solidity principle in order to survive; how two objects cannot exist in the same place, or move through each other, and how objects continue to exist when hidden from view. Specifically, we wanted to investigate, when faced with an obstructed goal, if children exhibit habituated action sequences (i.e. use trial-and-error learning), or if they explore the probable source of the causal problem. Hence our second set of hypotheses is:

- when an obstruction is blocking a goal, this will result in:
  - a longer time to attain the task goal;
  - more exploration;
  - the obstruction being touched first (rather than the goal itself when no obstruction).

If a child is like a scientist, they need to systematically test their hypotheses about the world by actively intervening in it in a targeted way (Kuhn and Dean Jr, 2004; Gopnik, 1996). So the structure of their exploratory behaviour

is important for making causal inferences, such as about what is behind a cover based on what is known already (Baldwin et al., 1993; Schulz et al., 2007). Hence in our final task we asked if individuals use information about hidden items to make causal inferences and direct their exploration. This led us to hypothesise that:

- when a cover hides certain areas of an object relative to when there is no cover at all, this will result in:
  - a longer time to attain the task goal;
  - more exploration;
  - a significant effect on the object area touched first (covered area or another area);
- and the same holds true when the cover hides an area of the object that is *directly* related to the task's goal, relative to when the cover instead hides an area indirectly related to the goal.

Exploratory behaviour is likely to become more structured with age to more efficiently generate, gather and integrate different types of information (Gibson and Pick, 2003; Karmiloff-Smith, 1995; Rochat, 2001). Hence our last research question is both qualitative and quantitative. Across different domains, how does exploration change with age to attain greater overall causal understanding? The tasks we pose are completely novel to all age groups, so all ages should explore for the same amount of information. So it stands to reason that the length of exploration may be similar across age groups, but the structure of exploratory behaviours (the diversity) may be more sophisticated in the older groups. Thus, our last set of hypotheses is as follows:

- within each experiment, on the first familiarisation trial, the older children are quicker to attain the task goal than the younger children;
  - there will also be an age effect on the time taken to attain the task goal in each experimental condition;
- within each experiment, once the task goal has been attained, younger children and older children explore all the experiments' apparatus for an equal amount of time;
  - however, older children display a greater diversity of exploratory behaviours than younger children in all the experiments;
- within each experiment, older children display exploratory behaviours that indicate use of more complex learning mechanisms, whereas younger children display exploratory behaviours that indicate use of more simple learning mechanisms;
  - so there is a qualitative developmental shift in the age at which these behavioural indicators are displayed in each experiment.

7.2 Methods

7.2.1 Participants

106 children (46 females, 60 males) aged 2–6 years-old (minimum 2 years, 2 months; maximum 6 years, 7 months) were recruited from and tested at two nurseries (ages 2–5 years) and one primary school (ages 5–6 years). These schools served working and middle classes in Birmingham, UK, but a range of ethnicities representing the diversity of the population participated. There was approximately the same number of children in each year group (Table 7.1). All of the participants were right-handed.

Table 7.1 – The number of females and males recruited from three institutions (two nurseries and one primary school) by age group. The total sample size for each age group is also shown.

Age (years)	Institution ID	Females	Males	*Total*
2	N1	7	9	*26*
	N2	4	6	
3	N1	2	6	*18*
	N2	5	5	
4	N1	1	2	*26*
	N2	2	3	
	S1	11	7	
5	N1	0	1	*18*
	S1	6	11	
6	S1	8	10	*18*

7.2.2 General protocol

We presented three experimental tasks involving different novel objects and physical problems to the school children, examining different aspects of exploration. All of the children experienced all the conditions of all the experiments, but in a counterbalanced order. All of the experiments had controls for any side biases. The experiments were conducted in a quiet area just outside of the classroom.

The tasks were presented to the children as games and for each game they completed, they received a sticker, whether or not they 'won' the game (attained the goal of the task). In each task, their exploratory behaviour was recorded in detail according to the ethogram described in Appendix C. The time taken to attain the task goal in the first familiarisation trial and in each of

the test trials was recorded. In Experiments 2 and 3, the apparatus[1] area/part touched first upon its presentation was also recorded. See subsection 7.2.4 and subsection 7.2.5 for details of what these apparatus areas were. There was little point to analyse this measure in Experiment 1, as, unlike Experiments 2 and 3, the key object property change in this experiment was invisible, so it would not be easily comparable (subsection 7.2.3).

We focussed on analysing the exploration data *after* the participant attained the task goal and constructed two general measures of exploration: the exploration duration and behavioural diversity (number of different exploratory behaviours) with each test apparatus. We did not analyse the exploration data before goal attainment, as here it would be difficult to distinguish between exploratory behaviours just for gaining information about the apparatus' properties and goal-directed exploratory behaviour for gaining information about how to attain the task goal. For instance, an increase in exploratory behaviours in one of the covered conditions of Experiment 3 (subsection 7.2.5) could just be explained by the participants needing to perform more actions to attain the task goal in getting a marble out, rather than increased interest in the possible affordances posed by a covered apparatus.

In each experiment, the child was first told the goal of the game, then in the first familiarisation trial, they were asked to try to attain the goal and they were encouraged to play with the toys as much as they liked. Then, whether the child succeeded or failed at the goal, the experimenter always demonstrated the correct action to ensure understanding of the goal. A second familiarisation trial was then run (followed by two more in Experiment 3, see

[1]Note that the term 'apparatus' is used interchangeably with 'object' in this chapter.

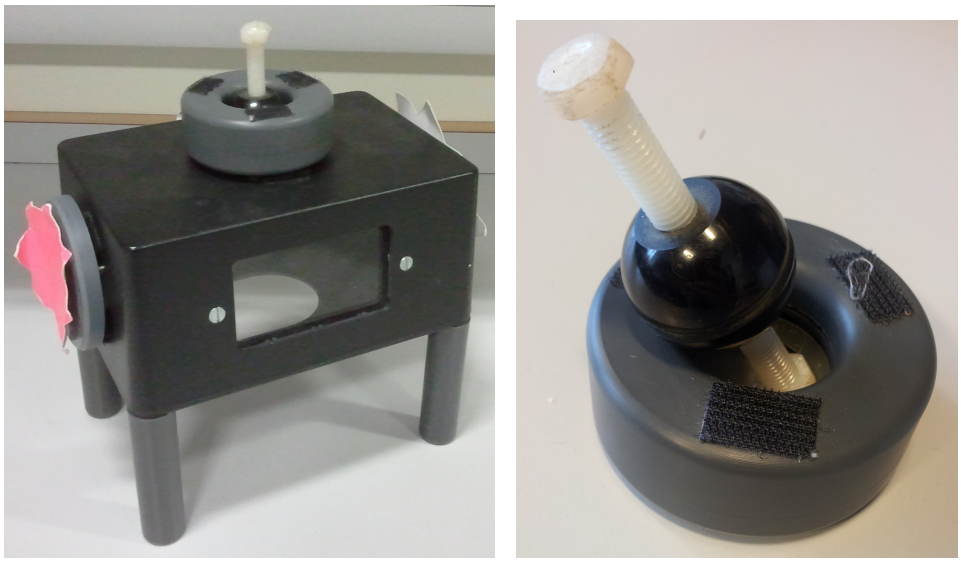
subsection 7.2.5). Subsequently, the test trials followed; one for each condition (see each experiment's details below). In-between the test trials, the experimental apparatus was prepared for the next condition out-of-sight of the participant, who was distracted to play with some popular classroom toys.

In each trial, the participant was allowed 30 seconds to attain the task goal, then 1 minute to explore the apparatus or for general play. If the child stopped interacting with the apparatus for more than 20 seconds before that time was up (e.g. out of boredom), this was noted and the experimenter moved onto the next trial. If the child did not attain the goal in a test trial, then any exploration after the 30 seconds was excluded from later analysis, but they were still allowed to play with the apparatus for the remaining minute and they still received a sticker. The experimenter then moved onto the next test trial as planned and continued recording from there.

7.2.3 Experiment 1: visible and invisible cues

Materials

The custom-made apparatus in this experiment was termed the 'push-pull box'. This was a hollow black plastic box on four legs with a transparent perspex 'window' on one side. There was a large hole at the bottom of the box and two round holes, one at the top and one to the side of the box (Figure 7.2.1a). The other key part of the apparatus was a black plastic ball with two handles embedded on opposite sides of the ball (Figure 7.2.1b). There was a thin groove along the midline of the ball. There was a rubber O-ring embedded in the ball's grey, round, plastic 'socket', which could fit into the ball's groove, thus holding the ball in place. The socket attached to the box with double-sided Velcro (Manchester, USA), at either the side hole, or the



(a) **(b)**

Figure 7.2.1 – Photos of Experiment 1's apparatus, the 'push-pull box, used for testing the influence of visible and invisible cues on exploration in children. **(a)** The overall apparatus (18 x 11 x 16 cm); **(b)** The removable ball (with embedded handles 9 cm in length) and its associated socket (7 cm overall diameter; 3 cm hole diameter; 3 cm height), which was could be attached either to the top of the side of the box by double-sided Velcro (Manchester, USA). Depending on which side of the socket the ball was put through, the ball could only either be pushed through, or pulled out of the socket. This was due to an O-ring (4 mm) fitted inside the socket, which slotted into the groove around the ball's midline and held it in place.

top hole.

The socket was reversible and could be attached to the box by either its upper side or its lower side. However, when placed in the socket, the ball could physically only be *pushed* through the socket on one of these sides. On the other side, to remove the ball from the socket, it had to be *pulled* out. When the socket was attached to one of the box's holes, the other hole was covered by a plastic disc, which was again held in place by Velcro. Two large colourful (yellow and pink) star-shaped stickers were stuck on this disc and the box's side without a hole in it, to make the box look more exciting for the

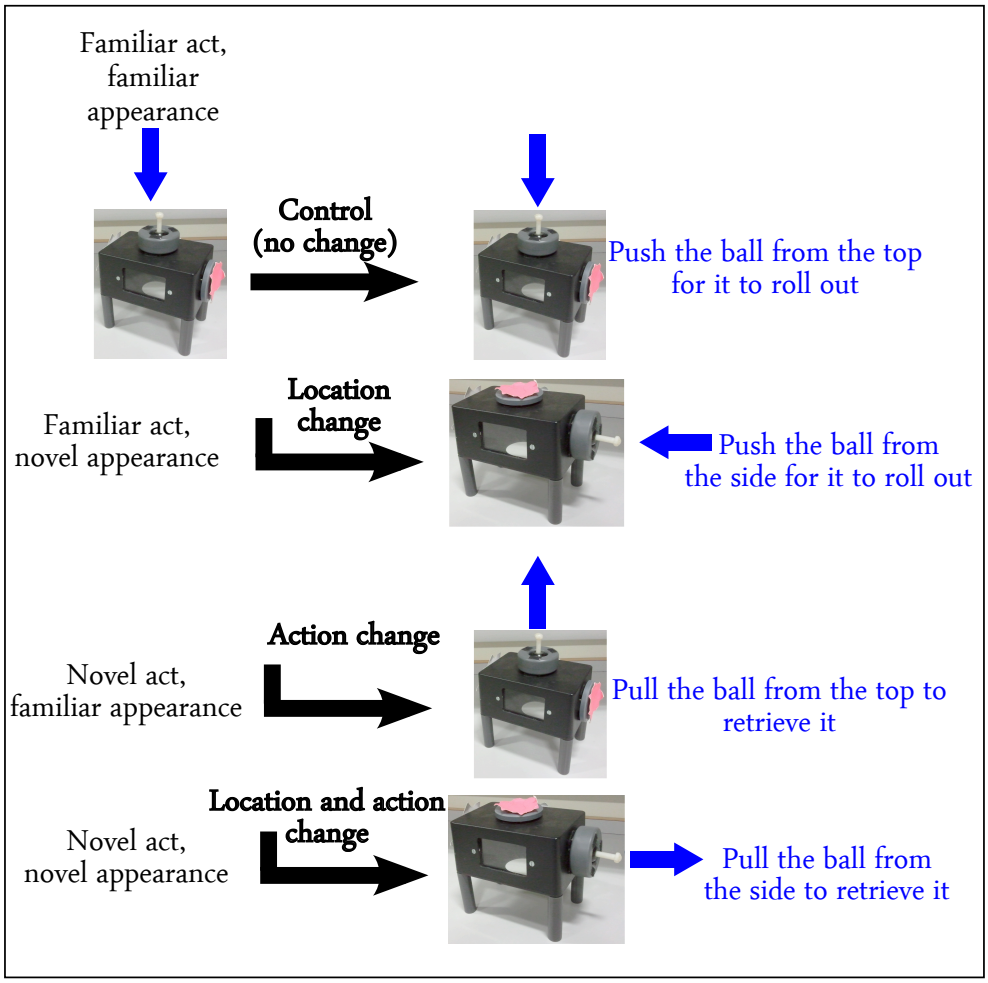


Figure 7.2.2 – A diagram of the conditions of Experiment 1 with the push-pull box on visible and invisible cues. The participants were all first familiarised with pushing the ball from the top of the box. Then they were presented with one of four conditions, which varied the novelty of the appearance (location of the ball/socket) and the action required (push/pull) to attain the ball. The blue arrows and words indicate the direction of the required action. The wording above each of the black arrows are the names of each of the conditions.

children.

Protocol

This experiment investigated the relative potential influence of invisible changes (i.e. required action) and visible changes (i.e. location of object parts) in an

object's affordances on exploration. The goal of this task was to retrieve the ball from the box. The apparatus was first set up with the socket on the top of the box, so the ball could only be pushed down through the hole. First, for an understanding of transparency, the experimenter tapped both sides of the box. All of the children were first familiarised with *pushing* the ball from the *top* of the box, so it fell out through the hole at the bottom (Figure 7.2.2). Then they were presented with one of four conditions, where the appearance of the apparatus and the action required to get the ball out was varied:

- **control no change condition**, as the ball was still on top of the box and the same push action was required as in the familiarisation trials;
- **location change condition**, where same push action was required, but the ball was now at the side of the box;
- **action change condition**, where the ball was still on top of the box, but now it had to be pulled to get out of the box;
- **location-and-action change condition**, where the ball was now at the side of the box and it had to be pulled.

The key question was whether the participant's exploration was more sensitive to the action change or to the location change. The script for this experiment is shown in Table 7.2.

7.2.4 Experiment 2: physical rules

Materials

The apparatus in this experiment was largely constructed out of a rectangular ring of multi-coloured pieces of Duplo® (Lego Group, Billund, Denmark), stuck to a cardboard base with double-sided tape, as shown in Figure 7.2.3.

Table 7.2 – Script for Experiment 1 on visible and invisible cues. For each trial for each condition, 30 seconds was allowed for task completion, then 1 minute was allowed for general exploration of apparatus.

1. "Let's play a game with this toy. See that ball? *[Ensure understanding]* Can you remove the ball from this box? Play with the toy as much as you like."

2. *If successful:* "Well done! Let me try... *[Demonstration of required action for that condition]* Can you retrieve the ball again?"

3. *If failed:* "Maybe you do it like this... *[Demonstration of required action]* Can you remove the ball from this box now? *[After successful action]*...and again?"

4. "Fantastic! Let me borrow this for a second, while you play with these toys." *(Change apparatus according to condition out of sight of the participant)*

5. "Can you get the ball out of the box again? Play with the toy as much as you like." *(Repeat from step 4 for each of the four conditions)*

6. "Well done! Here is your sticker. Would you like to play another game for another sticker?"

There was also a rigid, white cardboard tube and two Lego toy men (Billund, Denmark), who were stuck together at the feet by Araldite® (Huntsman Advanced Materials, Salt Lake City, USA).

The tube was of a length, that allowed it to fit snugly inside the Duplo ring, but a few fingers could easily fit in either side of the tube to lift it out. Lastly, there were two longer yellow Duplo blocks, which were removable from the rest of the apparatus. These were called the 'distractor block' and the 'obstructing block'. When the obstructing block was placed over the tube, as shown in Figure 7.2.3, it was not possible to get the tube out, without first lifting the obstructing block off. There was not enough space around the tube to allow this to occur.

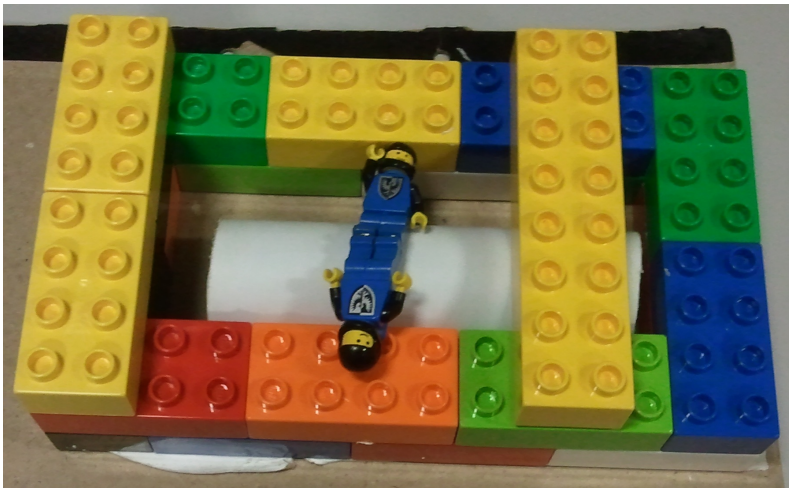


Figure 7.2.3 – A photos of the apparatus in Experiment 2 on physical rules, specifically object solidity. The entire apparatus was 22 x 13 x 5 cm, but the plastic white tube was 3 cm in diameter, 13 cm in length and 3 mm thick. The two yellow blocks (Duplo®, Lego Group, Billund, Denmark) on top were the distractor block and the obstructor block. Depending on the condition, the obstructor block either blocked the tube from being removed (on either the right or left side), or did not obstruct it. The Lego men were placed inside the tube.

Protocol

This experiment investigated whether individuals use physical rules (i.e. object solidity) or habituated action sequences (i.e. trial-and-error learning) to direct their exploration. The goal of this task was to get the toy men out of the tube, which was placed in the middle of the Duplo ring. A short storyline was created to make the game more interesting for the children. The toy men were space-men that had crash-landed their space-ship (the tube) in amongst some rocks (the Duplo pieces). It was made clear to the participants that they could touch or play with anything they liked (including the obstructor/distractor blocks). The familiarisation trials did not include the obstructing and distractor blocks, so the participant just had to pick up the tube, then tip it, for the men to fall out. When the obstructing and distractor blocks were introduced in the test trials, they were placed on top of the two

short ends of the Duplo rectangular ring (Figure 7.2.3). The distractor block never obstructed the tube, while the obstructing block did. The three conditions were as follows:

- **control no obstruction condition**, where the blocks are visible, each placed on the far ends of the ring, but not obstructing the tube;
- **left obstruction condition**, where the obstructing block was obstructing the tube towards the left end of the apparatus, and the distractor block was on the right end;
- **right obstruction condition**, where the obstructing block was obstructing the tube towards the right end of the apparatus, and the distractor block was on the left end.

Clearly, in the left and right obstruction condition, the obstructing block had to be first removed, before the toy men could be retrieved. The apparatus area touched first was recorded, whether it was the tube, obstructing block, distracting block, or another apparatus area (e.g. Duplo ring or cardboard base). The key question was whether the first response of the participant to an obstruction was to touch the goal, the tube, first (as if to follow through their previously familiarised sequence of actions), or if they touched the obstructing block first (as if to remove it). The script for this experiment is shown in Table 7.3.

7.2.5 Experiment 3: causal inferences

Materials

The custom-made plastic, grey apparatus in this experiment was termed the 'plunger box' and is shown in Figure 7.2.4. This was a rectangular box on

Table 7.3 – Script for Experiment 2 on physical rules. For each trial for each condition, 30 seconds was allowed for task completion, then 1 minute was allowed for general exploration of apparatus.

1. "Let's play this game with this toy. This game is about space-ships! Fred and John are brothers and they are both space-men *[Hold up Lego toy men]*. One day they were flying in their space ship *[Hold toy men within tube and 'fly them around']*, then they crashed - oh no! *[Put tube in Duplo hole]* Can you help free Fred and John from their space-ship? Play with them and anything else as much as you like." *(Obstructing and distractor blocks not present)*

2. *If successful:* "Well done! Let me try... *[Demonstration of required action for that condition]* Can you free Fred and John again?"

3. *If failed:* "Maybe you do it like this... *[Demonstration of required action]* Can you free Fred and John now?...and again?"

4. "Fantastic! Let me borrow this for a second, while you play with these toys." *(Attach distractor and obstructing blocks to apparatus according to condition out of sight of the participant)*

5. "Can you free Fred and John from their space-ship again? Play with them and anything else as much as you like." *(Repeat from step 4 for each of the three conditions)*

6. "Well done! Here is your sticker. Would you like to play another game for another sticker?"

four legs and its two long sides are transparent perspex. The box had two chambers, separated by a solid divider down the middle, one chamber of which had a hole in the bottom. The box's top was removable with a twisting motion, to allow the experimenter to put a marble in either chamber. Each marble was loosely secured in place by a small piece of Blu-Tack (Bostik, Paris-La Defense, France). Each of the box's short ends were attached to a plunger, which could be pushed into the box. The dark grey apparatus was placed on a white piece of card for greater contrast, so the hole could be seen clearly. Six colourful star-shaped stickers were stuck to the box in arbitrary, but consistent, locations to make it seem more exciting for the children. Initially, the apparatus was presented to the children with both plungers fully

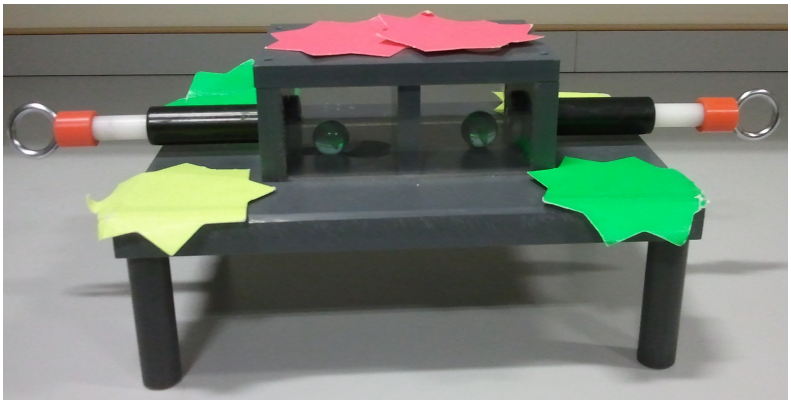


Figure 7.2.4 – A photo of Experiment 3's apparatus, the 'plunger box', for testing the role of causal inferences in exploration. The overall dimensions were 22 x 13 x 15 cm, or 36 cm in length when plungers were fully extended. The marble in each chamber was 1 cm in diameter. There was a hole for a marble to fall down in only one of the two chambers (here shown in the left chamber when facing the apparatus). The experiment could remove the top side with a twist. A piece of cardboard, big enough to cover one of the chambers, was placed on either side of the transparent 'windows' in the covered conditions.

pulled out. Two small pieces of black cardboard were also used to cover either perspex side when necessary, held in place by double-sided Velcro.

Protocol

This experiment investigated whether individuals use their knowledge about hidden items to direct their exploration. The goal of this task was to retrieve one of the marbles out of the box. The plungers could be pushed to move the marbles inside. As there was only a hole in one of the box's chambers, the participant could only retrieve a marble out of that chamber. So it is this chamber that is the 'object area directly related to the goal' (see hypotheses in section 7.1). The participant was not permitted to twist off the box's top (only three children attempted to).

Unlike the other two experiments, this experiment had four familiarisa-

tion trials: two where the hole was on the left side of the participant, and two where the hole was on the right side of the participant. Again, the order of these were counterbalanced across the participants. In the test trials, the black cardboard covers were introduced and the participants were told they could not touch the covers. The conditions varied where the covers were and on which side the hole was relative to the participant, as follows:

- **left control condition**, where both covers were stuck to the top of the box and the hole was on the left side of the participant;
- **right control condition**, which was the same as above, but on the right side;
- **left covered solid condition**, where the chamber with no hole was covered (the object area 'indirectly related' to the goal marble) and the hole was on the left side of the participant;
- **right covered solid condition**, which was the same as above, but on the right side;
- **left covered hole condition**, where the chamber with the hole was covered (the object area directly related to the goal marble) and the hole was on the left side of the participant;
- **right covered hole condition**, which was the same as above, but on the right side.

Clearly, when the hole was covered up, the child should causally infer that as they could see the chamber with no hole, then the covered chamber must contain the hole, so they must push the plunger next to the covered chamber. The apparatus area touched first was recorded, whether it was the correct plunger (next to the hole chamber), the wrong plunger (next to the solid chamber), or another ('non-plunger') area of the apparatus. The key question

Table 7.4 – Script for Experiment 3 on causal inferences. For each trial for each condition, 30 seconds was allowed for task completion, then 1 minute was allowed for general exploration of apparatus.

1. "Let's play another game with this toy. See the marbles there? *[Ensure understanding]* Can you retrieve one of the marbles from this box? Play with the toy as much as you like"

2. *If successful:* "Well done! Let me try... *[Demonstration of required action]* Great I did it! Let me borrow this for a second, while you play with these toys *[Out of sight of the participant, switch the side the hole is on facing the child round]* Can you remove one of the marbles out of the box again?"

3. *If failed:* "Maybe you do it like this... *[Demonstration of required action]* Great I did it! Let me borrow this for a second, while you play with these toys *[Out of sight of the participant, switch the side the hole is on facing the child round]* Can you remove one of the marbles out of the box now?"

4. "Fantastic! Let me borrow this for a second, while you play with these toys." *(Switch the side the hole is on)*

5. "Can you retrieval one of the marbles from the box again? Play with the toy as much as you like." *(Repeat from step 4 once more to finish the familiarisation trials)*

6. "Now let's put a small cover here and here. *[Put the covers on the apparatus according to the condition]* The new rule is you cannot touch these covers."

7. "Can you retrieve one of the marbles from the box now? Play with the toy as much as you like."

8. "Fantastic! Let me borrow this for a second, while you play with these toys." *(Move the covers on the apparatus according to the condition and repeat from step 7 for each of the six conditions)*

9. "Well done! Here is your sticker. Would you like to play another game for another sticker?"

was which plunger the participant touched first, especially when the chamber with the hole was covered. The script for this experiment is shown in Table 7.4.

7.2.6 General developmental analysis

We were also interested if there were any effects of age on each of the factors measured above. Each experiment examined different aspects of exploration

Table 7.5 – The criteria for task goal attainment and the behavioural indicators for complex learning mechanisms in each experiment. The text in italics indicates simple learning mechanisms. The last column states the condition in each experiment that is the key criterion condition to observe for the behavioural indicators.

Experiment	Task goal	Behavioural indicators	Key condition
1: visible and invisible cues	Get the ball out of the box	Explore action change more than location change *(vs. location more than action)*	(solely) action change
2: physical rules	Get the toy men out of the tube	Touch obstruction first *(vs. touch tube first)*	(left or right) obstruction
3: causal inferences	Get one of the marbles out of the box	Touch correct plunger first *(vs. touch wrong plunger first)*	(left or right) covered hole

and each asked a key question (see end of each experiment's protocol section above). From this, we asked whether these together could form different qualitative stages of development. Firstly, within each experiment, the time taken to attain the task goal with age was analysed, both for the first familiarisation trial and for each of the test trials. Secondly, within each experiment, we analysed the effect of age on exploration time and on exploratory behaviour diversity (after task goal attainment).

Lastly, we investigated how the first behavioural response to an object property change may change with age. A quantitative between-task analysis was not run, as the tasks were so different from each other, but they were compared qualitatively. A within-task analysis was run on the percent-

age of children that whether certain behavioural indicators were displayed within that experiment with age (Table 7.5). The 'task goal' was what the participants were explicitly told and demonstrated by the experimenter, i.e. what they thought they had to do to 'win the game'. Whereas, the behavioural indicators were the exploratory behaviour criterion that indicated the participant was using more complex learning mechanisms. If the participant performed the opposite behaviour criterion, this indicated they were using simpler learning mechanisms.

In Experiments 2 and 3, the behavioural criterion was when the participant touched the apparatus area highly relevant to the causal problem first, rather than the area less relevant to the causal problem. In Experiment 2, the causal problem was a solid obstruction, so the behavioural indicator was defined as: when the obstructing block was blocking the tube on its left or right side, then the participant touched the obstructing block first, rather than the tube. In Experiment 3, the causal problem was a hidden goal, so behavioural indicator was defined as: when the hole side of the apparatus was covered on the left or right side of the participant, then the participant touched the correct plunger first (next to the chamber with the hole), rather than the incorrect plunger. The criterion for Experiment 1 was slightly more complicated. The indicator here was when the participant (after the task goal had been attained) explored for longer when there had been an action change, rather than when there had been a location change. Exploration duration for the location-and-action change was discounted in this analysis.

7.2.7 Statistical methods

In each experiment, the time to attain the goal in the test trials and the exploration measures after the goal was attained (exploration duration and behavioural diversity) were analysed using a repeated measures General Linear Model. In each of these models, the experimental condition was included as a fixed factor, age was a random factor, and the possible interaction between the two was analysed. The assumptions of parametric methods (normality of error, homogeneity of variance and linearity) were confirmed from plots of coefficients versus fitted values. No transformations were required for these GLM models. All analyses were performed using Minitab® Statistical Software version 15.1.30. The probability level accepted for significance was $p < .05$.

Where significant effects were found and there were more than two levels within a factor, a series of post-hoc pair-wise Tukey tests were performed to find the source and direction of the significance. In all of the models, in addition to each experiment's condition factors (detailed in their respective subsections above), the following factors were included to check whether they had an effect on the general exploration measures: sex, school, time of day tested, date tested and test-and-trial order.

The measure of the apparatus area touched first in Experiments 2 and 3 was analysed using chi-square tests. Any significant effects found for this measure were analysed through a series of post-hoc pair-wise chi-square goodness-of-fit tests with a Bonferroni correction.

In the general developmental analysis, the measure of the time taken to

attain the task goal in the first familiarisation trial was analysed using model I linear regression. The exception was the within-task analysis of the different behavioural indicators of the underlying mechanisms, as it did not meet parametric assumptions. Therefore, it was analysed using a repeated measures Friedman test, adjusted for ties. As the data used for this analysis was proportional, it was arcsine-squareroot transformed.

7.3 Results

In all of the experiments, there were no significant effects or interactions of sex, school, time of day tested, date tested, or test-and-trial order. There was no significant difference in task goal attainment times in the last familiarisation trial and the control test trial in all experiments.

7.3.1 Experiment 1: visible and invisible cues

Time to attain task goal in test trials

The type of object property change had a significant effect on the amount of time to attain the task goal (GLM: $F_{3,320} = 249.04$; $p < .001$; Figure 7.3.1; Table 7.6). Post-hoc tests revealed the time taken to attain the task goal was significantly lower in the control condition than all the other three conditions (Tukey: all $p < .001$). However, no significant differences were found between the conditions where some object property change took place (Tukey: location vs. action vs. location-and-action; all $p > .05$).

Exploration after goal attainment

Once the task goal was attained, the type of object property change had a significant effect on the amount of time spent exploring the apparatus (GLM:

Table 7.6 – A summary table outlining the three GLM models for the effects of type of object property change on: the time taken (in seconds) to attain the task goal (i.e. goal time); the time (in seconds) spent exploring the apparatus after goal attainment (i.e. exploration duration); and the behavioural diversity (number of different exploratory behaviours) after goal attainment in Experiment 1. Test-trial order (1–24), sex and school (3 IDs) were included in all three models as fixed factors, while time of day tested and date tested were included as covariates. Object property (no change, location, location-and-action, action) was a fixed factor and age (in months) was a random factor in the models.

	Factor	**d.f.**	***F***	***p***
goal time	**Object property**	**3**	**249.04**	**<.001**
	Age	43	0.83	0.771
	Object property × Age	129	0.96	0.607
	Trial order	23	1.04	0.418
	Sex	1	1.82	0.178
	School	2	0.34	0.714
	Time	1	0.44	0.507
	Date	1	0.01	0.933
exploration duration	**Object property**	**3**	**37.95**	**< .001**
	Age	43	1.32	0.100
	Object property × Age	129	1.03	0.409
	Trial order	23	1.36	0.135
	Sex	1	0.00	0.998
	School	2	0.81	0.446
	Time	1	1.51	0.220
	Date	1	2.26	0.135
no. different exploratory behaviours	**Object property**	**3**	**46.63**	**< .001**
	Age	43	1.42	0.058
	Object property × Age	129	0.33	0.333
	Trial order	23	1.39	0.118
	Sex	1	2.61	0.108
	School	2	2.26	0.080
	Time	1	3.70	0.056
	Date	1	1.37	0.244

Significant variables are indicated in bold; $n = 424$ for all measurements.

$F_{3,320} = 37.95$; $p < .01$; Figure 7.3.2a) and on the diversity of exploratory behaviours performed on the apparatus (GLM: $F_{3,320} = 46.63$; $p < .001$; Figure 7.3.2b; Table 7.6). A series of Tukey post-hoc tests revealed the same pattern of results in exploration duration and behavioural diversity. The

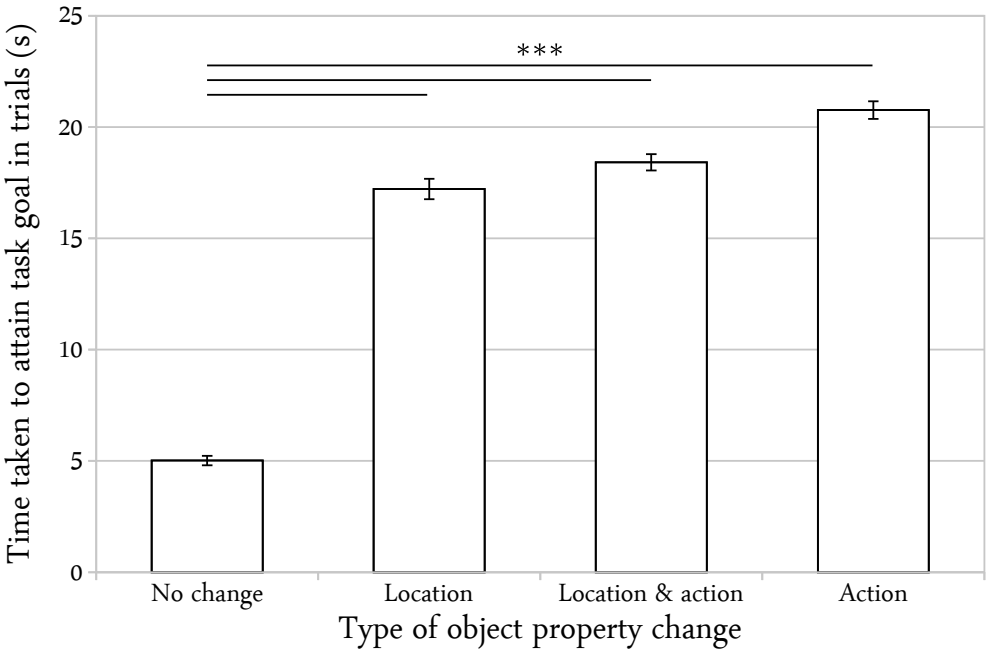


Figure 7.3.1 – A bar chart illustrating the time taken (in seconds) for the 106 children (aged 2–6 years) to attain the task goal in the test trials of each of Experiment 1's conditions, looking at the effect of visible and invisible cues on exploration. The conditions were based on changes to the 'push-pull box' shown in Figure 7.2.2, where either the appearance of the apparatus (location of the ball and socket), or the action required to attain the goal (push or pull the ball) was varied. In each trial, 30 seconds was allowed to attain the task goal, then 1 minute for general exploration. The error bars reflect the standard-error-of-the-mean. The line over each pair of bars indicates a significant difference was found between that pair at either $p < .05$ (*), $p < .01$ (**) or $p < .001$ (***; Tukey Test).

action change produced a significantly longer exploration time and greater behavioural diversity than the other three conditions (all $p < .001$). The control condition resulted in a significantly shorter exploration time and lower behavioural diversity than the location change and the combined location-and-action change ($p < .001$). However, there was no significant difference in the exploration duration and the behavioural diversity between the location change condition and the combined location-and-action change conditions ($p > .05$), although Figure 7.3.2 illustrates in both measures there was a tendency for the location-and-action change to be higher than the location change.

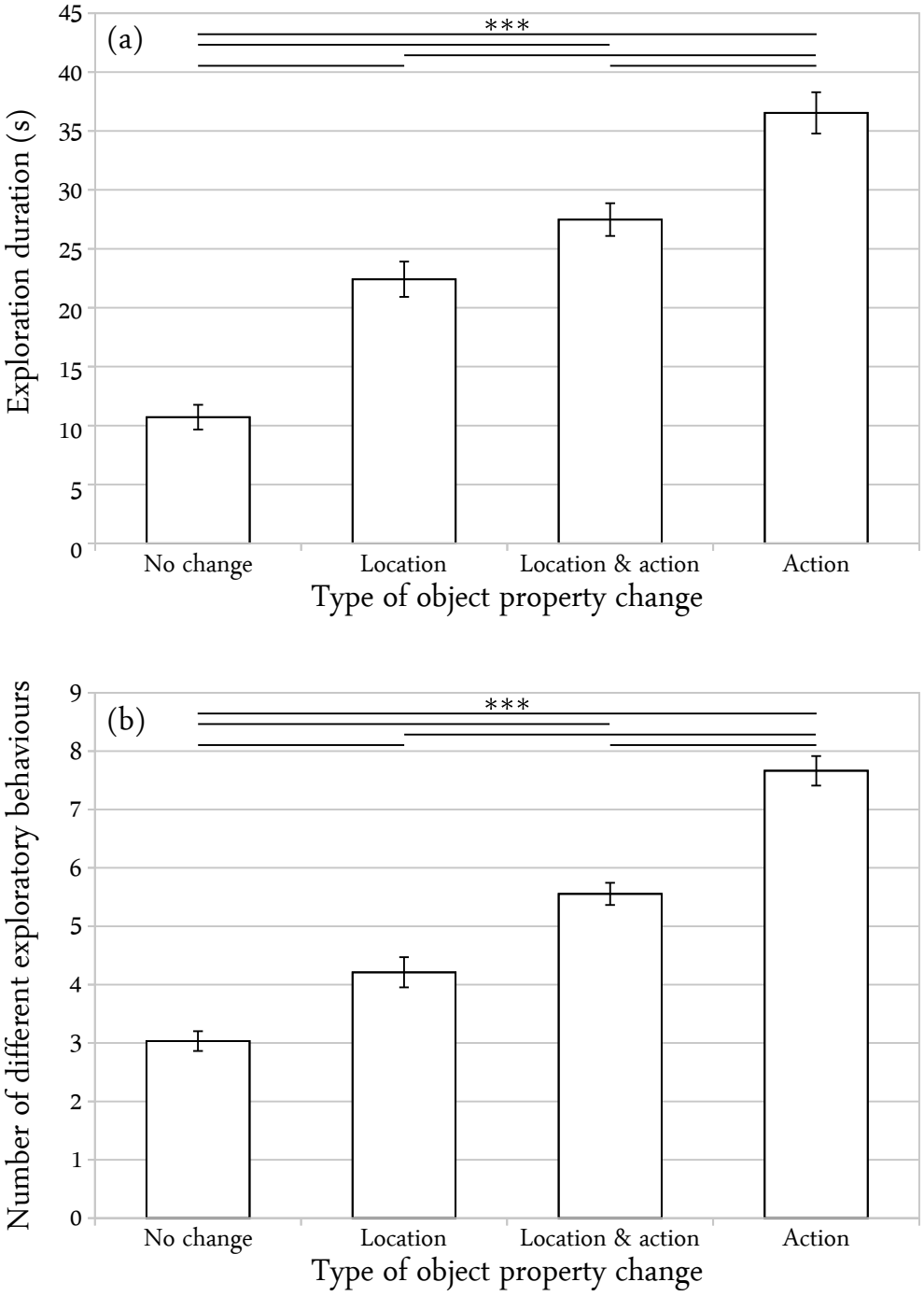


Figure 7.3.2 – Two bar charts showing the two general measures of exploration once the task goal had been attained in Experiment 1: **(a)** time (seconds) spent exploring the apparatus **(b)** behavioural diversity (number of different exploratory behaviours performed on the apparatus). The error bars reflect standard-error-of-the-mean. This figure caption corresponds to Figure 7.3.1.

Table 7.7 – A summary table outlining the three GLM models for the effects of an obstruction on: the time taken (in seconds) to attain the task goal (i.e. goal time); the time (in seconds) spent exploring the apparatus after goal attainment (i.e. exploration duration); and the behavioural diversity (number of different exploratory behaviours) after goal attainment in Experiment 2. Test-trial order (1–24), sex and school (3 IDs) were included in all three models as fixed factors, while time of day tested and date tested were included as covariates. Obstruction (no obstruction and obstruction conditions) was a fixed factor and age (in months) was a random factor in the models.

	Factor	**d.f.**	***F***	***p***
goal time	**Obstruction**	**1**	**114.22**	**< .001**
	Age	43	1.52	0.056
	Obstruction × Age	43	0.58	0.975
	Trial order	23	0.96	0.519
	Sex	1	0.01	0.907
	School	2	0.10	0.907
	Time	1	0.00	0.976
	Date	1	2.20	0.141
exploration duration	**Obstruction**	**1**	**250.19**	**< .001**
	Age	43	0.86	0.702
	Obstruction × Age	43	0.85	0.723
	Trial order	23	1.10	0.363
	Sex	1	1.27	0.263
	School	2	0.45	0.638
	Time	1	0.48	0.491
	Date	1	0.18	0.674
no. different exploratory behaviours	**Obstruction**	**1**	**196.92**	**< .001**
	Age	43	1.02	0.450
	Obstruction × Age	43	0.65	0.943
	Trial order	23	1.06	0.408
	Sex	1	3.77	0.055
	School	2	1.68	0.192
	Time	1	0.22	0.637
	Date	1	1.10	0.296

Significant variables are indicated in bold; $n = 212$ for all measurements.

7.3.2 Experiment 2: physical rules

Time to attain goal in test trials

The time taken to attain the goal was significantly higher in the obstruction condition than in the no obstruction condition (GLM: $F_{1,96} = 114.22$; $p < .001$;

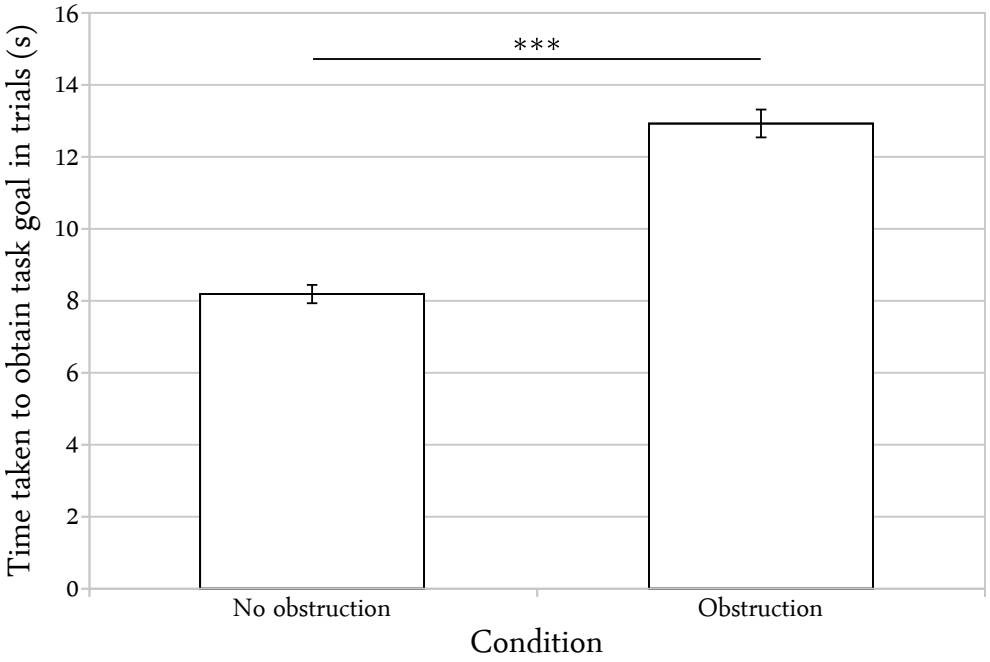


Figure 7.3.3 – A bar chart illustrating the time taken (in seconds) for the children to attain the task goal in the test trials of each of Experiment 2's conditions, looking at the effect of physical rules on exploration. The conditions were either when a obstruction blocked the goal, or it did not block it. This figure corresponds to Figure 7.3.1.

Figure 7.3.3 and Table 7.7).

Apparatus area touched first

Whether the tube was being obstructed or not had a significant effect on the apparatus area touched first ($\chi^2 = 20.805$, d.f. $= 3$, $n = 212$; $p < .001$; Figure 7.3.4 and Table 7.8). A series of pair-wise chi-square goodness-of-fit tests (with a Bonferroni correction, where $\alpha = 0.027$) revealed, firstly, when there was no obstruction, the tube was touched by significantly more participants than all the other apparatus parts (obstructing block, distracting block, or other part; all $p < .001$). No other significant differences were found in this condition between either of the blocks and the other parts (all $p > .05$).

Table 7.8 – A chi-square test was performed on the number of participants who touched different areas of the apparatus first in each of Experiment 2's conditions, where there was either no obstruction or there was an obstruction blocking the task goal. The apparatus areas are divided into the tube, obstructing block, distracting block, or another area. 'O' represents the observed counts, 'E' the expected counts, and 'C' the χ^2 contributions.

		Tube	Obstructor	Distractor	Other
None	O	59	22	21	4
	E	50.00	34.00	14.50	7.50
	C	1.620	4.235	2.914	1.633
Obstruction	O	41	46	8	11
	E	50.00	34.00	14.50	7.50
	C	1.620	4.235	2.914	1.633

$\chi^2 = 20.805, d.f. = 3, n = 212, p < .001$

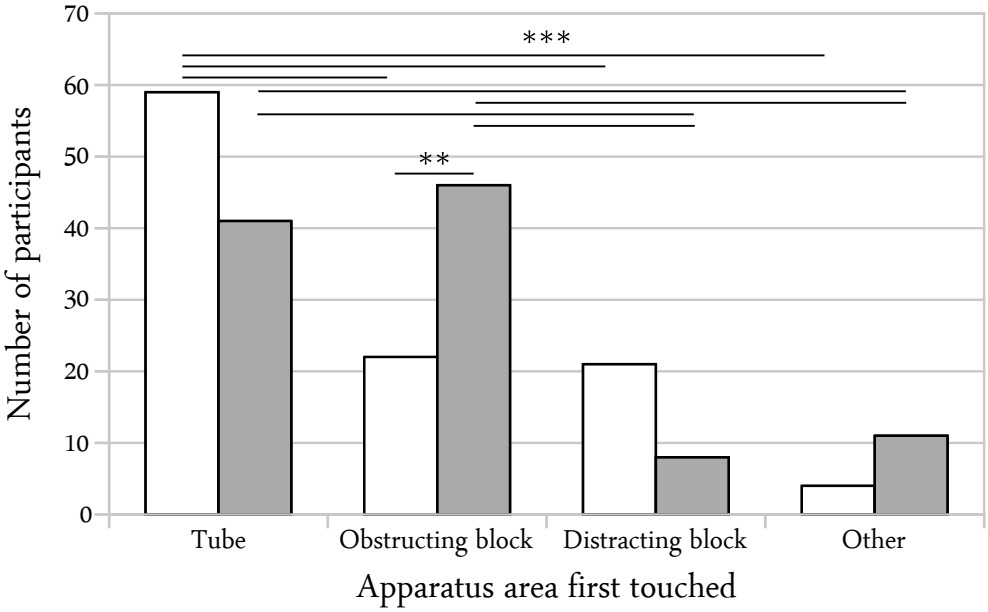


Figure 7.3.4 – A histogram showing the apparatus area touched first in each of Experiment 2's conditions, when there was no obstruction (white) and when there was an obstruction (grey) blocking the task goal. The apparatus is shown in Figure 7.2.3 and its areas are divided into the tube, obstructing block, distracting block, or another area (e.g. Duplo ring or cardboard base). The distractor block never obstructed the tube, while the obstructing block did. This figure corresponds to Figure 7.3.1, except that post-hoc tests were instead carried out using pair-wise chi-square goodness-of-fit tests with a Bonferroni correction (α = 0.027).

Secondly, however, when the obstructing block was placed on top of the tube, significantly more participants touched the obstructing block than when there was no obstruction ($\chi^2 = 8.47$, d.f. = 1, $n = 68$; $p = .004$). Moreover, both the obstructing block and the tube were touched by significantly more participants than the distracting block or the other apparatus parts (all $p < .001$). However, there was no significant difference in the number of participants that touched the obstructing block first and the number that touched the tube first ($\chi^2 = 0.29$, d.f. = 1, $n = 87$; $p = .592$).

Exploration after goal attainment

Once the task goal was attained, exploration time was significantly longer (GLM: $F_{1,96} = 250.19$; $p < .001$; Figure 7.3.5a) and there was a significantly greater diversity of exploratory behaviours (GLM: $F_{1,96} = 196.92$; $p < .001$; Figure 7.3.5b; Table 7.7) when there was an obstruction over the tube, than when there was no obstruction.

7.3.3 Experiment 3: causal inferences

Task goal attainment in test trials

Note this analysis only included participants who attained the goal within the allotted 30 seconds in all of the conditions. This was not an issue in the other experiments, where all of the participants attained the goals in the test trials. However, in this experiment, not all of the participants successfully retrieved a marble in the two covered conditions (so $n = 44$). Where the cover was placed on the apparatus had a significant effect on how long it took the children to attain the task goal of retrieving one of the marbles from the box (GLM: $F_{2,102} = 126.78$; $p < .001$; Table 7.9). As Figure 7.3.6 shows, the task goal took significantly longer to attain when the chamber with the hole was

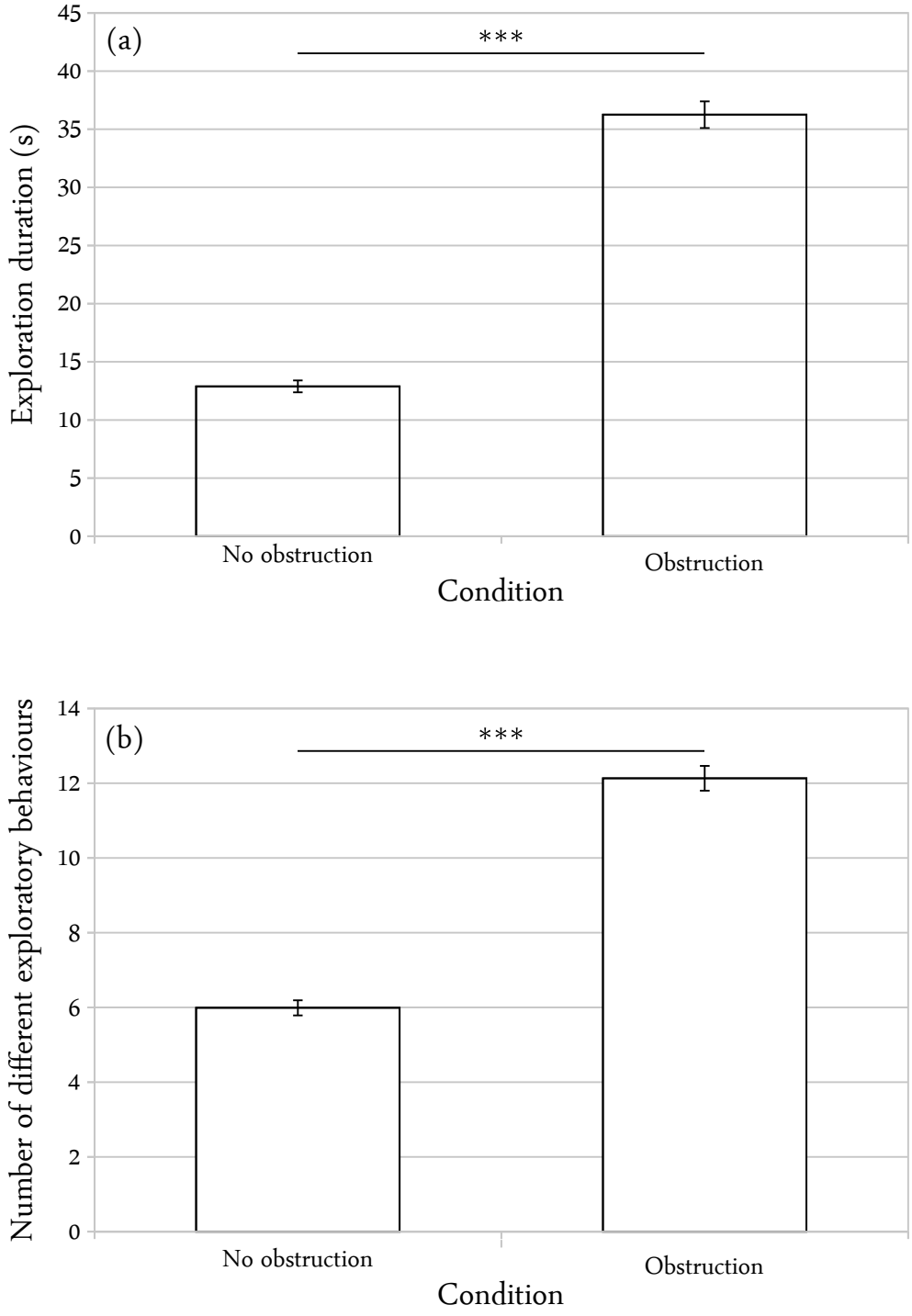


Figure 7.3.5 – Two bar charts showing the two general measures of exploration once the task goal had been attained in Experiment 2: **(a)** time (seconds) spent exploring the apparatus **(b)** behavioural diversity (number of different exploratory behaviours performed on the apparatus). An obstruction either blocked or did not block the goal. This figure caption corresponds to Figure 7.3.1.

Table 7.9 – A summary table outlining the three GLM models for the effects of box side covered: the time taken (in seconds) to attain the task goal (i.e. goal time); the time (in seconds) spent exploring the apparatus after goal attainment (i.e. exploration duration); and the behavioural diversity (number of different exploratory behaviours) after goal attainment in Experiment 3. The first model only took account of the participants who attained the goal within the allotted 30 seconds in all of the conditions. Test-trial order (1–24), sex and school (3 IDs) were included in all three models as fixed factors, while time of day tested was included as a covariate. The date tested was included as another covariate in the last two models. Cover (no cover, solid side covered and hole side covered) was a fixed factor in the models. Age (in months) was included as a random factor in the last two models.

	Factor	**d.f.**	***F***	***p***
goal time	**Cover**	**2**	**126.78**	**< .001**
	Trial order	23	1.03	0.436
	Sex	1	1.15	0.285
	School	2	0.15	0.858
	Time	1	2.04	0.156
exploration duration$^{\diamondsuit}$	**Cover**	**2**	**300.13**	**< .001**
	Age	43	1.05	0.404
	Cover × Age	86	0.86	0.774
	Trial order	23	0.60	0.926
	Sex	1	0.38	0.539
	School	2	0.77	0.465
	Time	1	0.28	0.598
	Date	1	0.04	0.849
no. different exploratory behaviours$^{\diamondsuit}$	**Cover**	**2**	**179.04**	**< .001**
	Age	43	0.64	0.955
	Cover × Age	86	1.26	0.098
	Trial order	23	1.01	0.455
	Sex	1	0.93	0.337
	School	2	0.39	0.675
	Time	1	3.19	0.076
	Date	1	0.23	0.715

Significant variables are indicated in bold. $^{\diamondsuit}n = 132$
$^{\diamondsuit}n = 318$

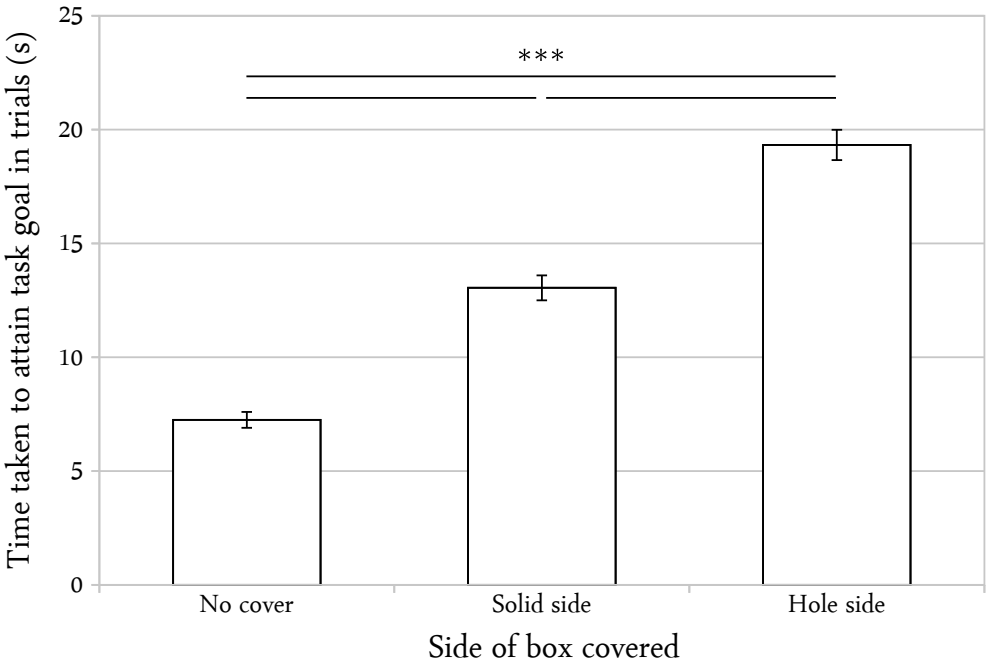


Figure 7.3.6 – Time taken to attain goal in test trials of Experiment 3's conditions.A bar chart illustrating the time taken (in seconds) for the children to attain the task goal in the test trials of each of Experiment 3's conditions, looking at the effect of causal inferences on exploration. Experiment 3's apparatus was the 'plunger box' shown in Figure 7.2.4. The conditions varied the location of the covers on the plunger box, so either placed in a control location on top of the box ('no cover condition'), over the side with a hole for a marble to fall out, or over the side without a hole ('solid side'). This figure corresponds to Figure 7.3.1.

covered, than when the solid chamber was covered, or than the control, when neither chamber was covered (Tukey: both $p < .001$). Additionally, when the solid chamber was covered, the goal attainment time was significantly longer than the control condition (Tukey: $p < .001$).

Apparatus area touched first

The side the cover was on had a significant effect on the apparatus area first touched ($\chi^2 = 56.335$, d.f. $= 4$, $n = 318$; $p < .001$; Figure 7.3.7; Table 7.10). A series of pair-wise chi-square goodness-of-fit tests (with a Bonferroni correction, where $\alpha = 0.023$) revealed, firstly, when there was no cover (control

Table 7.10 – A chi-square test was performed on the number of participants who touched different areas of the apparatus first in each of Experiment 3's conditions, where there was either no cover, a cover over the solid side, or a cover over the hole side of the apparatus. The apparatus areas are divided into the correct plunger (next to the hole side), the wrong plunger (next to the solid side), and the non-plunger area. 'O' represents the observed counts, 'E' the expected counts, and 'C' the χ^2 contributions.

		Correct	**Wrong**	**Non-plunger**
None	O	78	12	16
	E	51.67	28.00	26.33
	C	13.422	9.143	4.055
Solid	O	47	23	36
	E	51.67	28.00	26.33
	C	0.422	0.893	3.549
Hole	O	30	49	27
	E	51.67	28.00	26.33
	C	9.086	15.750	0.017

$\chi^2 = 56.335, d.f. = 4, n = 318, p < .001$

condition), significantly more participants touched the correct plunger first (on the hole side), rather than the wrong plunger or another area of the apparatus (both $p < .001$). In this condition though, there was no significant difference between the number of participants that touched the wrong plunger first and the number of participants that touched another (non-plunger) area of the apparatus first ($\chi^2 = 0.57$, d.f. = 1, $n = 28$; $p = .450$).

Secondly, however, in the condition where the solid chamber was covered (i.e. the marble next to the hole was showing), significantly more children touched a non-plunger area of the apparatus first than in the control condition ($\chi^2 = 7.69$, d.f. = 1, $n = 52$; $p = .006$). Within this condition, the only significant difference was between those that touched the correct plunger first

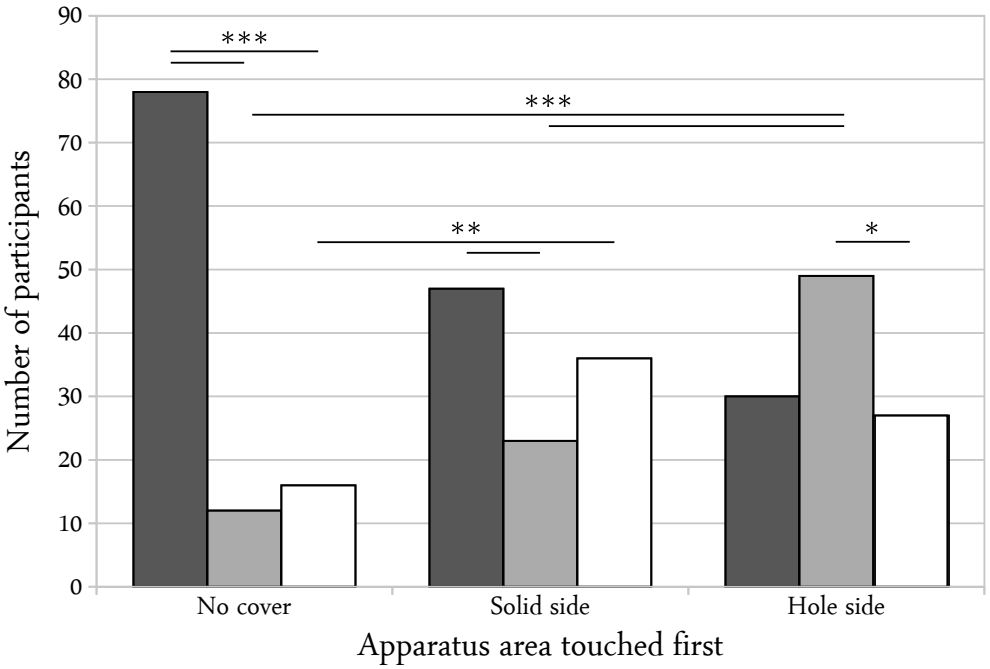


Figure 7.3.7 – A histogram showing the apparatus area touched first in each of Experiment 3's conditions, when there was no cover, a cover over the solid side, or a cover over the hole side of the apparatus shown in Figure 7.2.4. The apparatus areas are divided into the correct plunger (next to the hole side; dark grey), the wrong plunger (next to the solid side; light grey), or a non-plunger area (white). This figure corresponds to Figure 7.3.1, except that post-hoc tests were instead carried out using pair-wise chi-square goodness-of-fit tests with a Bonferroni correction ($\alpha = 0.023$).

and those that touched the wrong plunger first ($\chi^2 = 8.23$, d.f. = 1, $n = 70$; $p = .004$).

Lastly, in the condition where the chamber with the hole was covered, significantly more children touched the wrong plunger first than in either of the other conditions (both $p < .001$). Also, within this condition, the number touching the wrong plunger was significantly higher than those who touched a non-plunger area of the apparatus first ($\chi^2 = 6.37$, d.f. = 1, $n = 76$; $p = .012$) and (nearly significantly) higher than those who touched the correct plunger first ($\chi^2 = 4.57$, d.f. = 1, $n = 79$; $p = .033$). There was no significant difference

found between these latter two groups (χ^2 = 0.16, d.f. = 1, n = 57; p = .691).

Exploration after goal attainment

Once the task goal was attained, the side of the box covered had a significant effect on the amount of time spent exploring the apparatus (GLM: $F_{2,158}$ = 300.13; p < .001; Figure 7.3.8a; Table 7.9) and the diversity of exploratory behaviours performed on the apparatus (GLM: $F_{2,158}$ = 179.04; p < .001; Figure 7.3.8b). A series of Tukey post-hoc tests revealed the same pattern of results in both exploration duration and behavioural diversity, where there were significant differences between all the conditions (all p < .001). The most exploration occurred when the chamber with the hole was covered, followed by when the solid chamber was covered, and the least exploration occurred when there was no cover at all.

7.3.4 General developmental analysis

Task goal attainment on first familiarisation trial

We analysed the age of the child with their time taken to attain the task goal on the first familiarisation trial within each experiment. In each experiment, there was a significant relationship between age and the goal attainment time (linear regression: Expt. 1, $F_{1,104}$ = 251.05, p < .001, R^2= 0.71; Expt. 2, $F_{1,104}$ = 66.44, p < .001, R^2= 0.39; Expt. 3, $F_{1,104}$ = 57.89, p < .001, R^2= 0.36; Table 7.11).

As the children became older, they took a shorter amount of time to attain the task goal. From Figure 7.3.9, we can see the causal inferences task (Experiment 3) seemed to be the hardest task to solve, whereas the obstruction task (Experiment 2) seemed to be the simplest to solve.

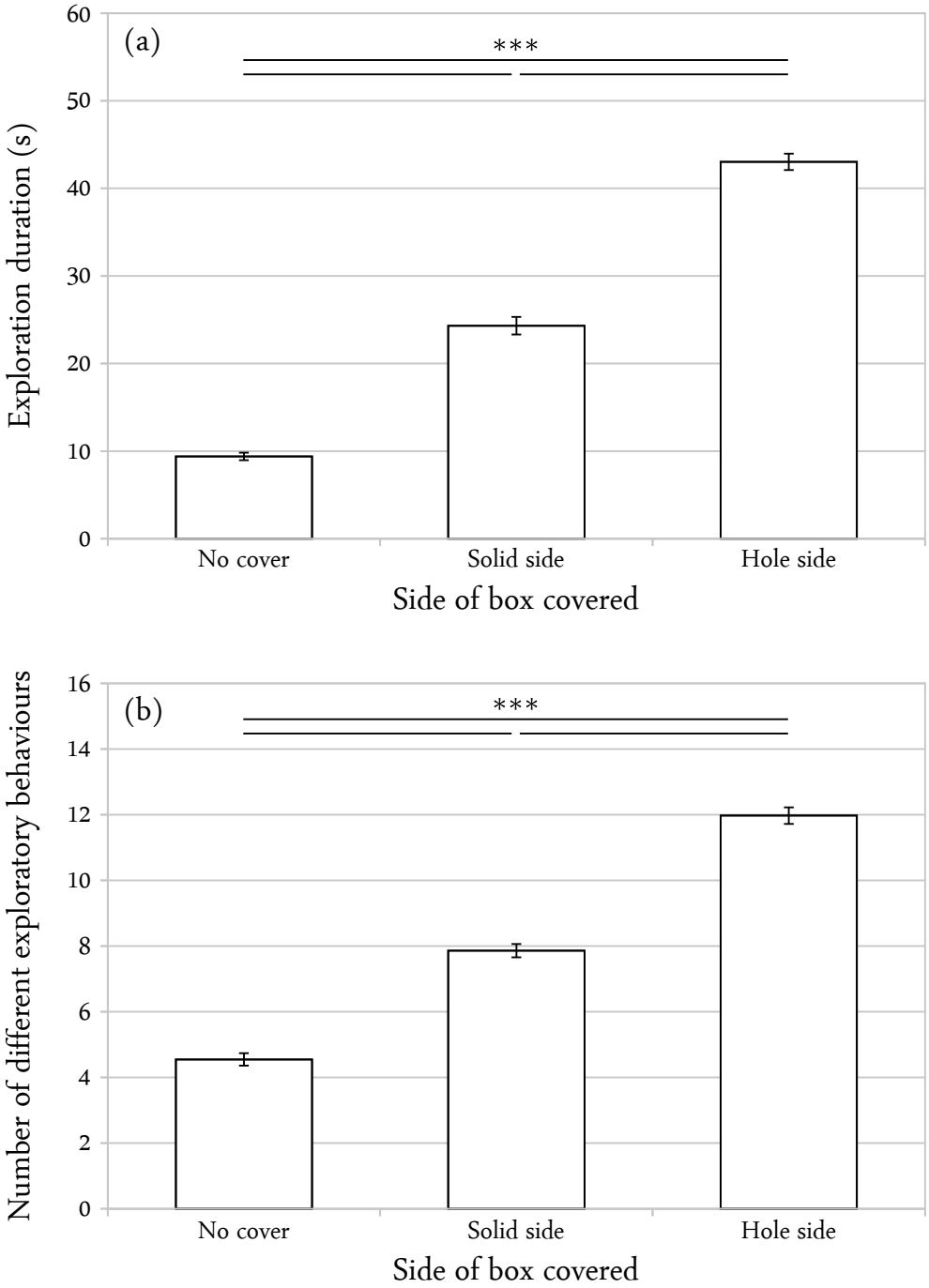


Figure 7.3.8 – Two bar charts showing the two general measures of exploration once the task goal had been attained in Experiment 3: **(a)** time (seconds) spent exploring the apparatus **(b)** behavioural diversity (number of different exploratory behaviours performed on the apparatus). There was either no cover, or a cover over the solid side or the hole side of the apparatus shown in Figure 7.2.4. This figure caption corresponds to Figure 7.3.1.

Table 7.11 – A summary table outlining the linear regression models for the relationship between age (in months) and the time taken to attain the task goal on the first familiarisation trial within each experiment.

Expt. no.	Factor	Coefficient	*T*	*S*	R^2	d.f.	*F*
1	Constant	36.847 (1.289)	28.58				
	Age	-0.375 (0.024)	-15.84				
	Regression			**4.019**	**0.71**	**1**	**251.05**
2	Constant	19.744 (1.160)	17.03				
	Age	-0.173 (0.021)	-8.15				
	Regression			**3.614**	**0.39**	**1**	**66.44**
3	Constant	34.380 (1.242)	27.69				
	Age	-0.173 (0.021)	-7.61				
	Regression			**3.870**	**0.36**	**1**	**57.89**

Standard errors are reported in parentheses; $p < .001$ for all measurements.

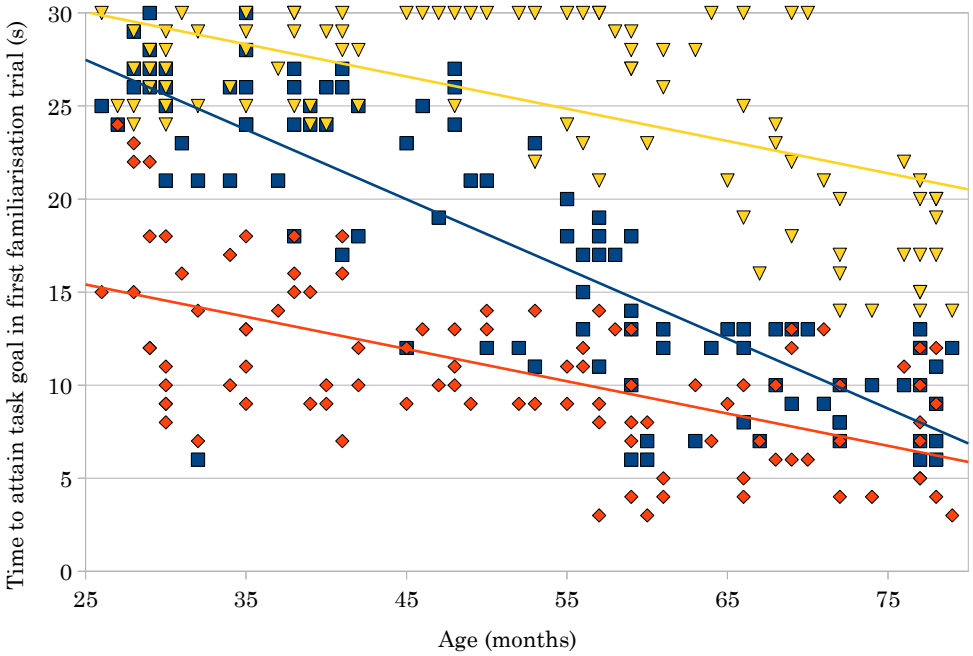


Figure 7.3.9 – A scatter plot illustrating the time taken to attain the task goal on the first familiarisation trial of all three experiments against age (2–6.5 years). The data for Experiment 1 is represented by the blue squares; Experiment 2 by the red diamonds; and Experiment 3 by the yellow triangles. A linear regression line has been plotted for each experiment in their respective colours: Expt. 1 R^2= 0.71; Expt. 2 R^2= 0.39; Expt. 3 R^2= 0.36.

Task goal attainment on test trials

There was no significant age effect on the time taken to attain the goal in the test trials of Experiment 1 (GLM: $F_{43,320} = 0.83$; $p > .05$; Table 7.6), or of Experiment 2 (GLM: $F_{43,96} = 1.52$; $p > .05$; Table 7.7). Due to the large number of younger participants excluded from Experiment 3's analysis (subsection 7.3.3), age effect on task goal attainment in this experiment's test trials was not analysed.

Exploration after goal attainment

There was no significant age effect on time spent exploring the apparatus after the task goal was attained in the test trials of Experiment 1 (GLM: $F_{43,320} = 1.32$; $p > .05$; Table 7.6), Experiment 2 (GLM: $F_{43,96} = 0.86$; $p > .05$; Table 7.7), and Experiment 3 (GLM: $F_{43,158} = 1.05$; $p > .05$; Table 7.9). No significant age effects were found for behavioural diversity in the test trials of either Experiment 1 (GLM: $F_{43,320} = 1.42$; $p > .05$; Table 7.6), Experiment 2 (GLM: $F_{43,96} = 1.02$; $p > .05$; Table 7.7), or Experiment 3 (GLM: $F_{43,158} = 0.64$; $p > .05$; Table 7.9).

Behavioural indicators of underlying mechanisms

A Friedman analysis (adjusted for ties) was conducted on the proportion of children that displayed the indicators at each experiment at each month of age. This analysis found both a significant effect of the age at which children displayed the indicators in the experiments (Friedman: $S_{53} = 98.27$; $p < .001$), and a significant effect of the experiment type that the children displayed the indicator in (Friedman: $S_2 = 58.21$; $p < .001$; Table 7.12).

Figure 7.3.10 illustrates how indicator display within each experiment

Table 7.12 – A summary table outlining the Friedman analysis on the proportion of children that displayed the behavioural indicators for underlying simple and complex learning mechanisms at each experiment at each month of age. This proportional data was arcsine-squareroot transformed.

Factor	Grand median	d.f.	S	S (adj.)
Age	60.68	53	$60.42^{\diamondsuit}$	$31.26^{\sun}$
Experiment	71.75	2	$98.27^{\sun}$	$58.21^{\sun}$

$^{\diamondsuit}p = 0.225$ $^{\sun}p < .001$

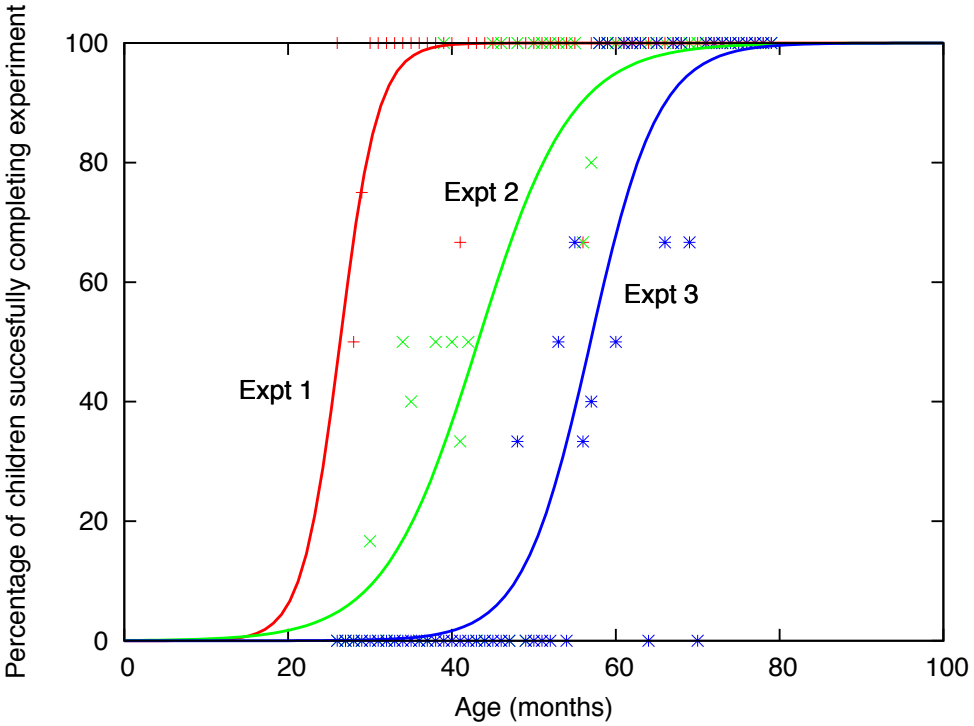


Figure 7.3.10 – Developmental curves for the behavioural indicators of underlying learning mechanisms being displayed in Experiment 1 (red plus data-points), Experiment 2 (green cross data-points), and Experiment 3 (blue star data-points). Cumulative frequency lines have been added for each experiment to guide the eye, each fitted using least-squares.

seems to shift with age. Note that due to the spread of the data-points, the lines in this figure are simply there to guide the eye. Nearly all of the children by 2 years of age could already display the indicator for Experiment 1. Then by 3 years, all of the children could display for Experiment 2, followed by Experiment 3 being displayed by 5 years of age.

7.4 Discussion

The three aspects of exploration we tested seem to occur consecutively in development. We found children explored more when there were invisible changes in an object, as opposed to more visible changes. Also they explored more when a solid obstruction across a task goal was introduced. Further, as the children became older, they increasingly touched the obstruction first, rather than another area of the apparatus. Children further seemed to utilise previous knowledge and explored more when an object was hidden. In studying the exploratory behaviour in these different contexts, we can begin to discuss two related points. Firstly, how the different underlying learning mechanisms of children change with age and what they are. Secondly, we can consider how varying the type of problem affects the strategy they employ to gather different types of information.

7.4.1 Visible and invisible cues

In Experiment 1, as hypothesised, children explored for longer and performed a wider diversity of exploratory behaviours when there was an invisible change in the action required to get the ball out of the box. This was relative to when the ball visibly changed location from the top to the side of the box, and even when there was a combined location-and-action change. However, in disagreement with our hypotheses, there was no significant difference in

both exploration measures between the combined location-and-action and just the location change conditions, although a slight trend was observed (Figure 7.3.2). Any change in the apparatus did result though in a longer time to retrieve the ball from the box, as hypothesised. This last finding is to be expected, as once the child realised they could not follow through with their previously learned action sequence, naturally they then took longer to work out how to solve the same problem in a different way.

This suggests children are more sensitive, or at least more interested, in invisible changes in an object, rather than visible changes. The invisible change in this case was the action required (afforded) by the apparatus to retrieve the ball from the box, from a push action to a pull action. Greater exploration occurred once the ball was attained, perhaps to discover why this change had occurred, while the initial appearance of the apparatus remained the same. On the other hand, a location change, while still interesting (as it still produced more exploration than no change at all), does not necessarily alter the functional properties of the apparatus. Nonetheless, the visible cues were more important to the children's exploration than we predicted, as it is intriguing there was no real difference between the visible location change and the combined visible and invisible location-and-action change. Perhaps this is because a visible change cues the child to expect that an affordance change is likely to have also occurred. Whereas, in solely the action change condition, there was no such visible cue, so when it was discovered an invisible change had taken place, it is was unexpected.

It is a common finding across the animal kingdom that any change in the environment produces more exploration (reviewed in Power, 2000). Devel-

opmental psychologists frequently take advantage of this phenomenon by creating impossible causal events in the expectancy violation procedure (e.g. in Hood et al., 2000). Perone et al. (2008) found children focus their exploration more on action changes, rather than changes in appearance. They argued this was because actions performed on an object provide more information about its affordances and function. It could also help children categorise objects, which, in turn, is important for forming different internal causal representations about the world (Arriola-Rios et al., 2013).

Even infants have been shown to be sensitive to different object categories through their exploration (e.g. Oakes et al., 2012). Schulz et al. (2008) demonstrated how children explore an unexpected, within-category change more than an expected between-category change. In our study, the within-category change could be argued to be the action change, while the between-category change could be argued to be the combined location-and-action change. However, we must be careful with interpreting an action change producing more exploration because of its potential functional properties. So further studies are needed to disambiguate the reasons for why children explored more in this kind of problem-solving context.

7.4.2 Physical rules

Consistent with our hypotheses of the second experiment, when an obstruction was introduced to block the goal (rather than when just present but not blocking), children explored for longer and displayed a wider variety of exploratory behaviours once they attained the goal. The obstruction also induced a longer time to attain the goal in the test trials that, as in the first experiment, is not very surprising (subsection 7.4.1). Finally, again in accord-

ance with our hypotheses, when there was no obstruction, the tube (which contained the goal) was touched first, as the children had learned in the previous familiarisation trials. Whereas, once the obstruction actually blocked the tube, a greater number of children touched the obstruction itself first than in the no-obstruction condition. However, contrary to our hypotheses, an equal number of children still touched the tube first in this obstruction condition.

When presented with an obstruction, if an individual is using simple learning mechanisms to obtain the goal, then it is likely the individual will try to do the same action sequence they had previously learned in the familiarisation trials (touch the tube first). Whereas if they have existing knowledge or an 'internal rule' about object solidity (Spelke, 2000), then they are more likely to explore the obstruction first, to try to find a solution to obtaining the same goal. There may be a longer latency to the first exploration bout as they try to 'reason' through the problem, but we did not analyse this. The finding, that greater exploration occurred in the obstruction condition after they attained the goal, is further evidence that some sort of object solidity rule is aiding their causal learning*.

However, approximately half the children still touched the tube first even in the obstruction condition, which points to simpler, trial-and-error learning mechanisms. This may just be because a physical rule has not been acquired yet in their development, which indeed seems to be the case, as discussed later in subsection 7.4.4. Alternatively, perhaps these children did have the conceptual capacity to understand the causal implications of the obstructing block, but were not able to exercise full inhibitory control* (Simpson and

Riggs, 2007; Simpson et al., 2012). To be able to stop impulsive, prepotent responses (e.g. if extensively reinforced) is pivotal to successful problem-solving, and so it has been the interest of developmental psychologists and animal cognitive scientists alike (e.g. Hood et al., 2006; Vlamings et al., 2010). It fully develops between 3 to 5 years of age (e.g. Gerstadt et al., 1994), which relates to a significant portion of our sample size. It should also be noted the exploratory focus was on the obstructing block, rather than the identical distracting block, so it was not just the presence of the block that caused more exploration.

Such a solidity rule would be important not just for human children to develop, but for a range of animal species (Kundey et al., 2010). It would aid them, for instance, in navigating around obstacles, being vigilant against hidden predators, or finding embedded food items. These constants in the world are fairly predictable (Arriola-Rios et al., 2013). So they can be genetically encoded (Dittrich et al., 1998; Spelke, 2003; Csibra and Gergely, 2007; Taylor et al., 2010; Withagen et al., 2012), then built on and refined within an individual's lifetime (e.g. in other great apes; Cacchione et al., 2009; Cacchione and Call, 2010). While it is generally agreed that such rules are present in human children, the details are still under debate (e.g. Karmiloff-Smith, 1995; Hood et al., 2000; Baillargeon, 2002).

Moreover, the children who touched the tube first, may have simply been exploring whether the tube could still move freely enough to allow it to be removed anyway, such as up the sides – although this was not possible. Another issue is that these children may have been afraid to change anything about the apparatus that the experimenter changed.

7.4.3 Causal inferences

In our last experiment, in accord with our hypotheses, children took longer to attain the task goal, longer to explore once they attained it, and performed a greater diversity of exploratory behaviours when certain areas of the apparatus were covered, than when there was no cover. All these effects were even more pronounced when the apparatus' chamber with the hole in it (directly related to the goal) was covered, rather than the chamber that was solid and had no hole (indirectly related to the goal) was covered. Lastly, as hypothesised, the location of the cover had a significant effect on the apparatus area touched first. Specifically, first with no cover, more children touched the correct plunger first as they had in the familiarisation trials. However, when the cover was introduced but the hole could still be seen, more children touched a non-plunger area first than in the last condition, but even more children still touched correct plunger first. Whereas, when the hole was hidden, most children touched the wrong plunger first. In this condition, approximately the same number of children touched a non-plunger as those who touched the correct plunger first.

These results suggest children use their previous knowledge and explore more when objects are hidden. This may have been prompted by uncertainty in the missing or ambiguous information present (Inglis, 1983; Beck et al., 2008; Bonawitz et al., 2012a; Arriola-Rios et al., 2013). Some of the children clearly had some difficulty though when the hole was covered. This may point towards an 'out-of-sight, out-of-mind' error, but an understanding of object permanence* has been shown to exist in infants as young as 3-months-old (e.g. Baillargeon and DeVos, 1991). Therefore, like in Experiment 2 (subsection 7.4.2), it is more probable some of the children had deficits in

inhibitory control, especially as this was essentially a binary task. The goal was 'retrieve one of the marbles from the box', so if one of the marbles was visible, it would be especially hard for the child to resist the impulse to try out the wrong plunger first.

Alternatively, it may be because some of the children did not yet have the ability to causally infer; i.e. 'if the chamber showing has no hole, then the hole must be in the hidden chamber, so I must press the plunger next to the hidden chamber'. However, this capacity has again been displayed by very young children in other studies (e.g. Das Gupta and Bryant, 1989). Causal inferences have been shown to be central to problem-solving abilities and to influence exploratory behaviour (Schulz, 2012). A future study should analyse what exploratory behaviour sequences children of different ages exhibit in such contexts. For instance, perhaps younger children are more perserverative* in their actions (e.g. Stahl and Pry, 2005), which could indicate more trial-and-error learning mechanisms at work.

Nonetheless, it is compelling that many of our participants touched a non-plunger area first when a cover was introduced – even more than the wrong plunger in the hole-covered condition. Perhaps the exploration results in this experiment reveal children often note a causally important change has occurred and so they widen their strategy, such as in what areas they attend to. Therefore, it would be interesting to analyse more specifically what non-plunger parts they explored and how they explored them. Further conditions could also be designed, such as covering up only part of each chamber. Then other measures could be recorded, such as which perspectives the child uses in exploring different sides of the apparatus in different conditions.

7.4.4 General developmental analysis

Generally, the time taken to solve each task's goal in the first familiarisation trial decreased with age, which agrees with our hypotheses. Experiment 2 seemed to be easier to solve than Experiments 1 and 3, the latter of which was the most complex. However, we found no similar effect of time for attaining the task goal in the test trials. A second effect, against our hypotheses, was that no developmental effect was found for behavioural diversity. There was no effect of age on exploration time either, which was predicted. Lastly, we would like to tentatively suggest we found each aspect of the exploration measured by each of the experiments seemed to occur consecutively in development. All the children displayed the behavioural indicator (potentially for complex learning mechanisms) in Experiment 1 by 2 years old, in that they explored the action change more than the location change. Then from 4 years of age, in Experiment 2 they touched the obstruction first. Finally in Experiment 3, all children aged 5 years or older touched the correct plunger first, even when the hole was covered.

The exploring individual should seek out information to reinforce, evolve and, where possible, prove or disprove its current internal representations, particularly if its expectations are violated, such as in some of the tasks in our study (Chappell et al., 2012). Exploration has been shown to be made up of different underlying constructs (e.g. McReynolds et al., 1961; Vandenberg, 1984), and the idea of distinct cognitive domains is not a new one (e.g. Fodor, 1983; Karmiloff-Smith, 1995; Carruthers, 2006; Callebaut and Rasskin-Gutman, 2005; Shettleworth, 2012). Each domain may involve information being processed in different ways (Arriola-Rios et al., 2013). Different exploration domains are often interleaved, such as in alternating between eating

and playing with food. This allows knowledge of different domains to develop roughly in parallel (Bushnell and Boudreau, 1993). Then, when switching domains, the individual is able to group bits of information together according to the current domain involved (Demery et al., 2010).

For those domains not developed in parallel, certain abilities may only come online much later in life. Competences gained at one developmental stage, can later be revised or transformed at a later developmental stage (Karmiloff-Smith, 1995). Depending on the individual's needs and competences, a specific, relevant subset of experiences allow specific, relevant features of its ecological niche to be captured (e.g. von Bayern et al., 2009). We believe there is continual extension of these 'information blocks' throughout the individual's life (Demery et al., 2010; Chappell et al., 2012; Arriola-Rios et al., 2013). At different developmental stages, a human child likely takes in different aspects of the same overheard conversation, or different aspects of the operation of the same tool, then later adapts accordingly (see discussion in Sloman, 2010).

However, it is not clear whether the displayed behavioural indicators in each of our experiments is due to the development of different exploration domains, or due to increasing task complexity. The latter explanation is suggested by our other finding of goal attainment time shown in Figure 7.3.9. We cannot say for sure, for instance, how exactly the structure of exploration changes from one developmental stage to the next, or how each domain apparently reflected in each experiment interact with each other. It is also questionable whether we can really compare each of these experiments using this measure (on one graph as in Figure 7.3.10). The criterion for these

behavioural indicators in each task was quite a subjective judgement, even if it was supported by logical reasoning and previous work (Table 7.5; section 7.1). Nonetheless, our findings do have compelling implications, not just from a developmental perspective, but also from an information-processing perspective, warranting further investigation.

The absence of an age effect, found for exploratory behavioural diversity and exploration duration in all of the tasks, may just be due to too small a sample size in each age group. It may be advantageous to increase the time allowed to explore the apparatus in future work. Alternatively, perhaps the three sets of apparatus simply had limited affordances, which restricted the number of actions they provided for. For a better comparison across the tasks, a more standardised measure of behavioural diversity should be used, as each set of apparatus afforded different types of actions and, potentially, a different number of actions. Alternatively, as suggested above in subsection 7.4.3, perhaps analysing different exploratory behaviour sequences would be a better measure.

It is also important to remember development does not stop at sexual maturity. Human adults continually learn and refine their hypotheses about how the world works throughout their lives (Rheingold, 1985; Demery et al., 2010; Arriola-Rios et al., 2013). So the field would benefit from more studies on adult exploration.

7.4.5 Comparison to parrot exploration

Traditionally, the methodological approach for studying cognitive development in human and non-human animals has been very different, but a com-

parative approach can be very informative, especially if a bottom-up approach is taken (de Waal and Ferrari, 2010; Chittka et al., 2012). Buchsbaum et al. (2012) believe humans' extended altricial period* has allowed us to become particularly flexible* exploratory learners and great causal inferrers. They argue other animals rely on simpler learning mechanisms and only a few have developed highly specialised complex learning abilities for solving problems specific to their ecological niche, such as the food-caching western scrub jay (*Aphelocoma californica*; Raby et al., 2007). Nonetheless, several animals living in dynamic environments do display quite sophisticated cognitive capacities (e.g. Huber and Gajdon, 2006), arguably to the same degree of flexibility as in humans.

Although from quite different ecological niches, both parrots and humans are animals that have evolved in risky, ever-changing environments. It is advantageous for both to develop efficient information gathering and processing mechanisms. As described in chapter 6, we conducted a series of behavioural tests on the highly exploratory kakariki (*Cyanoramphus novaezelandiae*) using a similar protocol to this study, but only using simple objects. Like the children in Experiment 1 (subsection 7.4.1), kakariki explored more and performed a wider diversity of exploratory behaviours when there were invisible, functional changes in an object, rather than visible changes.

Kakariki and children may be accomplishing these similar tasks using qualitatively different mechanisms (Demery et al., 2010; Chappell et al., 2012; Arriola-Rios et al., 2013). Our brains may allow us to solve more advanced tasks quicker than a kakariki (e.g. making tools), but a kakariki may outperform us in other domains (e.g. navigating through a canopy).

7.4.6 Summary

We exploited the strong exploratory tendencies of human children, by presenting them with three tasks involving different novel objects and physical problems, to provide a window into the mechanisms and strategies they used in causal learning. As with a previous series of comparative experiments with parrots, we found individuals pay more exploratory attention to invisible changes than visible changes in an object. Moreover, children are sensitive to physical principles governing the behaviour of objects, such as when they detect an obstruction, they direct their exploration accordingly to find a solution. They similarly seem to utilise exploration to gather information about hidden items.

Lastly, we would like to tentatively suggest each of these experiments has measured different exploratory domains, which seem to fully come 'online'* at different stages of cognitive development. Each of these exploratory domains could be argued to map onto each of the consecutive stages of our Three-stage Theory of Exploration (Demery et al., 2010; Arriola-Rios et al., 2013). Experiment 1 looked at the possible sensory predispositions a child may have to the visible and invisible cues in an object, which would be important for directing exploration in the first stage. This is when the child is forming hypotheses about the world. Experiment 2 focussed on the physical rules a child may have for understanding how the world works, which we described as being integral to the second stage. This is when the child is testing their hypotheses about the world using targeted exploratory behaviours. Finally, Experiment 3 investigated causal inferences, which can be used in the final stage to abstractly fill in the gaps of knowledge. This is when the child is refining and extending their hypotheses about the world, which continues

throughout life.

Kakariki certainly seem to complete the first stage of exploration (i.e. sensitivity to visible and invisible cues), as well as elements of the second stage (e.g. exploration directed by unexpected changes, but not physical rules like in this study; chapter 6). Comparatively, in this study we have found evidence human children – at least certainly from 5 years-old and within these domains – complete the final stage of our theory, as well as the first two. There are aspects of the theory that we have not yet investigated, such as meta-cognition and learning generalisation. We have barely begun to understand how exploration can support different individuals' learning about the world around them. Many more studies are needed to verify the Three Stage Theory of Exploration, and to extend our findings to other species and other environmental contexts.

CHAPTER 8

Conclusions

THIS thesis has taken a multi-faceted approach to understanding information-processing in animals, particularly the parrot. It considered how the sensorimotor system can be adapted for exploration and how the environmental information it gathers impacts it. This led to a reflection on how the animal may have different cognitive adaptations for exploratory learning to solve different environmental problems. This was investigated through a series of comparative behavioural experiments, using both parrots and human children.

Firstly, in considering the sensorimotor adaptations for exploratory learning, it was found that parrot visual fields are unlike any other birds' measured to date, and seem to be tightly integrated with the haptic perception provided by the bill tip organ (chapter 2). Parrots also seem to be strongly lateralised, both visually and motorically (chapter 3 and chapter 4). Psittacine exploration was divided into two broad phases: approach to an object

of interest (dominated by visual exploration), followed by manipulation of that object (dominated by haptic exploration).

Visual perception of a distant target object does not appear to be hampered by parrots' distinctive climbing mode of locomotion, where the bill acts as a third appendage (chapter 3). The object seems to be identified first in a monocular field, but on approach visual control is transferred to the binocular field, until the object is within grasping distance of the parrot. Subsequently, during the exploratory manipulation phase, the bill seems to be the predominant manipulatory appendage, supported by the feet (chapter 4).

Further studies are needed to investigate how these senses are integrated to provide cross-modal information about objects. Of particular interest is how exploration is affected when one of these senses are impaired, and whether information gathered through one modality can be passed to another. Measuring which part of an object is explored by each of these senses would be revealing. This could be done using eye-tracking (techniques beginning to develop in Kjaersgaard et al., 2008; Voss and Bischof, 2009), or objects embedded with pressure sensors (e.g. Campolo et al., 2009). A cruder measure would be to design the object with an impressionable surface (like the Polymorph used in chapter 6).

Secondly, in considering the environmental influences on exploration, it was found that the enrichment of a parrot's housing conditions strongly affected their exploratory behaviour, both in terms of the diversity of behaviours displayed and their duration (chapter 5). The impact of this upon the bird's cognitive performance is not as yet entirely clear and requires fur-

ther testing. What is apparent is that any conclusions drawn from captive animal cognitive tests, should consider whether the results hold ecological validity. The dangers of extrapolating from captive animals to wild animals is a known issue (e.g. Thornton and Lukas, 2012). In the light of our work, one might conclude that as wild birds are presumably maximally enriched, they may outperform captive birds. Alternatively, the additional stresses wild birds are subjected to (e.g. predators and food availability) may have a negative effect. Either way, habituation effects further compound the situation.

This thesis could not examine the effect of enrichment on chicks because of the failure of the unenriched group to breed, but this should certainly be considered in future. The results with adults suggests parrots raised in an enriched environment display greater understanding of the world around them. Cognitive development in chicks has been shown to be measurable not just qualitatively, but quantitatively as well (e.g. Funk, 2002; Fox and Millam, 2004). Experiments should be designed to compare the speed and diversity of development of enriched versus unenriched chicks. Further experiments (potentially in the field as well as the laboratory) should then test the dependency of problem-solving abilities on enrichment – that is whether being given more complex toys encourages birds to solve more complex problems.

Lastly, in considering the cognitive and behavioural strategies of exploration, it was found that, with both parrots (chapter 6) and human children (chapter 7), exploration increases when the object of interest behaves in unexpected ways. This is consistent with the theory proposed by Demery et al. (2010) and Arriola-Rios et al. (2013); that individuals carry around with them

a set of beliefs or views about how the world and objects in it behave, and that it is when these beliefs are violated that greater exploration ensues. Moreover, it seems greater importance is afforded to unexpected changes relating to the functionality of an object, rather than to superficial changes, such as colour. This increased curiousity is manifested in terms of greater exploration times and behavioural diversity. Exploration strategies were seen to change over a period of several days, presumably as the parrots refined their hypotheses about how the world works (Demery et al., 2010; Arriola-Rios et al., 2013). However, it is unclear how a longer period of time (i.e. several months or years) would affect this exploration pattern. Longitudinal studies into how individuals extend their knowledge in different exploratory domains would be revealing (like in Rusher et al., 1995).

Similar results were found in children, but their exploration also seemed to be driven by their internal physical rules and causal inferences about hidden environmental features. An interesting additional test for children would be to measure whether they are capable of realising that they have gaps in their knowledge (Demery et al., 2010; Arriola-Rios et al., 2013). Counterfactual thinking studies, such as those conducted by Beck et al. (2008), could illuminate this. Moreover, exploratory tendencies seem to persist throughout humans' lifetimes (Rheingold, 1985; Daw et al., 2006). How strategies alter and are refined beyond maturity is a compelling question, though one which fell beyond the remit of this thesis. Before wider conclusions can be drawn about exploration, other species need to be tested to see if the general pattern holds.

In conclusion, exploratory behaviour is not random, but structured, se-

lective and sensitive to particular categorical features of the environment. One issue that applies to all of these studies, is that the sequence of behaviours should be analysed (like in Renner and Seltzer, 1991, 1994). The behaviour pattern should indicate some detail of the underlying strategy, which in turn would reveal an element of the animal's cognitive processes. Specifically, the perseveration, diversity, flexibility and selectivity of behaviour patterns should be explored, particularly in reference to environmental enrichment and when different causal problems are faced. A second issue is that these non-invasive tests are unable to directly determine the processes occurring within animal minds. Artificial intelligence provides a tool by which we can propose and test models of animal cognition without the need for neural measures (e.g. Chappell and Hawes, 2012b; Arriola-Rios et al., 2013; Appendix E). Nonetheless, while this thesis has only just begun to scratch the surface of exploratory learning, its distinctive interdisciplinary approach has potential to reveal the underlying mechanisms of how different animals understand the world around them.

Part IV

Appendices

APPENDIX A

List of publications and conference posters

A.1 Publications

Demery, Z. P., Chappell, J., & Martin, G. R. (2011). Vision, touch and object manipulation in Senegal parrots *Poicephalus senegalus*. *Proceedings of the Royal Society B*, **278**, 3687–3693. doi:10.1098/rspb.2011.0374

Demery, Z., Arriola-Rios, V. E., Sloman, A., Wyatt, J., & Chappell, J. (2010). Construct to Understand: Learning through Exploration. In *Proceedings of the International Symposium on AI-Inspired Biology* (pp. 59–61).

Chappell, J., Demery, Z. P., Arriola-Rios, V. E., & Sloman, A. (2012). How to build an information gathering and processing system: lessons from naturally and artificially intelligent systems. *Behavioural Processes*, **89**(2), 179–186. doi:10.1016/j.beproc.2011.10.001

Arriola-Rios, V. E., Demery, Z. P., Wyatt, J., Sloman, A., & Chappell, J. (2013). Salient Features and Snapshots in Time: An Interdisciplinary Perspective on Object Representation. In G. Dodig-Crnkovic & R. Giovagnoli (Eds.), *Computing Nature* (*Studies in Applied Philosophy, Epistemology and Rational Ethics*, Vol. 7, pp. 171–184). Berlin, Heidelberg: Springer-Verlag. doi:10.1007/978-3-642-37225-4_10

A.2 Posters

Symposium on Natural/Unconventional Computing and its Philosophical Significance at the AISB/IACAP World Congress 2012: 'Construct to understand: learning through exploration'.

Association for the Study of Animal Behaviour Summer Conference 2011, University of St. Andrews: *'Learning through exploration – a bird's eye view'*

Central European University Conference on Cognitive Development 2012, Budapest: *'How can children inform our understanding of exploratory learning in non-human animals?'*

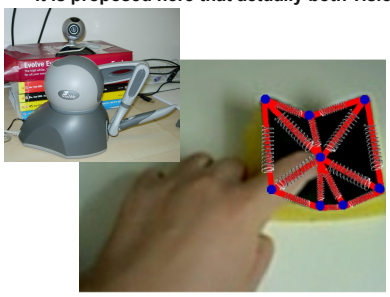
Construct to Understand: Learning through Exploration

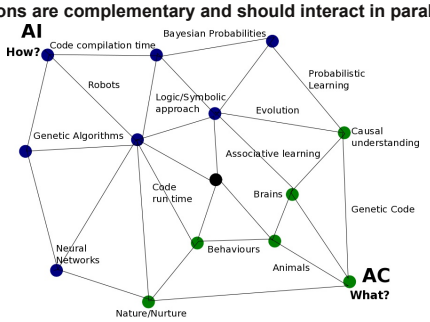
Towards a collaboration between the fields of Artificial Intelligence and Animal Cognition

Zoe Demery, Veronica E. Arriola Rios, Jackie Chappell, Jeremy Wyatt & Aaron Sloman

zxd878@bham.ac.uk v.arriola-rios@cs.bham.ac.uk

- Artificial Intelligence (AI) and Animal Cognition (AC) share a common goal: to study learning and causal understanding.
- However, the fields seem completely different: while AC studies intelligent systems present in nature, AI tries to to build them practically from scratch.
- It is proposed here that actually both visions are complementary and should interact in parallel to better achieve their ends.





Artificial Intelligence (AI)

(-) Computers are fast to execute predesigned algorithms, but can't reason alone
(-) Learning is not automatic, it must be programmed
(-) No robot can yet flexibly generalise the acquired knowledge to new situations
(-) Still don't know how to abstract concepts from the environment
(-) Technology can not yet replicate complex human behaviours
(+) Computers can run simulations of animal behaviours that could otherwise be unethical
(+) Robots force us to explicitly define the design of the model, allowing for very concrete testable experimental hypotheses
(+) Gives an insight into the interaction between the internal representation (i.e. brain) and the environment
(+) Allows investigation of the evolution of different behaviours
(+) We explicitly know how the 'robot brain' was coded, while we often can't directly observe all the processes of the animal brain in situ

Animal Behaviour & Cognition (AC)

(-) Difficult to separate within-trial simple learning from causal reasoning
(-) Spontaneous behaviour is difficult to analyse, even if it is potentially very revealing
(-) Similarly, many conclusions are often based on a very small sample size.
(-) We can only infer about the cognitive processes by directly observable behaviour
(-) Failures to complete a task can be just as illuminating as the successes
(-) Is qualitative or quantitative data more interesting?
(-) Can't talk to non-human animals about their introspection like we can with humans
(+) A wide range of real-life biological (often complex) models can be studied directly in a variety of contexts and species
(+) Non-human animals provide a useful comparative basis for testing the development of cognitive theories
(+) Emphasis on systematic, scientific investigation with experimental manipulation both in the lab and field

Common Problems & their Inter-disciplinary Answers

Anthropocentricity:
The way humans behave is not the ultimate answer, as other ecological niches can stimulate unique competences.
In modelling cognition a single model is not enough, so collaboration between different mechanisms may be required with no anthropocentric bias.

Confusing terminology:
Quite frequently the same terms in both fields refer to very different concepts, or similar concepts are called different names,
e.g. *neural nets* or *learning*.

Broaden Horizons:
Both fields can help each other if researchers are open to learning and understanding the ideas and initially daunting new terminology proposed by the other field.

Different points of view:
There is always more than one way to phrase a question and considering different angles of the situation can provide a more complete answer,
e.g. *top-down* (AC) vs. *bottom-up* (AI).

An example problem: how does an individual learn about the deformability of objects?

Applying the Three-stage Theory of Exploration

1. Forming Hypotheses
- Probabilistic reasoning and simple trial-and-error learning with genetic predispositions to particularly salient environmental features, e.g. edges and corners.
- Represents and segregates the world in general categories.

2. Testing Hypotheses
- Progressively uses more complex mechanisms like causal reasoning, so actions less repetitive but behaves more flexibly.
- Tests internal theories and rules of object relations by performing certain actions on certain objects.

3. Extending & Refining Hypotheses
- Analyses theories and re-uses knowledge about the world by combining them in similar but new situations.
- Fill in gaps in knowledge abstractly by causal inferences.
- Hypotheses are extended throughout life.

AI

Method:
- *Propose* a set of candidate mass spring models for every material the robot encounters.
- *Search* for the model that best fits the data the robot acquires through selective interactions with the material.
- *Test* the system by consecutively presenting the robot with simple solid and deformable novel objects.
- *Evaluate* the quality of the generated models and the number of steps it took to find them.

Hypothesis 1:
It is possible to generate a geometrical internal representation on top of which a mass spring physical model can be applied[1][2].
The nodes of the mesh can be placed at points of high curvature.

Hypothesis 2:
It is possible to calibrate the parameters of the model by using a random search algorithm.
This algorithm samples the space of possible parameters and selects the most suitable ones.

Hypothesis 3:
It is possible to improve learning using a clustering algorithm that learns to segment the physical model's space of parameters, so the appropriate models for new materials are calibrated faster.

AC

Method:
Consecutively present individual parrots with novel objects of different shapes and deformabilities. Then record in detail their actions.

Hypothesis 1:
Higher frequency of touching the corners and areas of high curvature over the smooth surfaces.

Hypothesis 2:
Explores a novel deformability more than a familiar one.
Between trials, the individual begins to explore the most compressible and the most rigid objects more than others of intermediate deformability, but they progressively focus in detail on these intermediate levels.

Hypothesis 3:
The parrots eventually reach a point where they have so much experience with the different objects' compressibility and affordances, that they can combine their understanding of the different objects to solve a new task.

REFERENCES
[1] D. Morris. Automatic Preparation, Calibration, and Simulation of Deformable Objects. *Computer Methods in Biomechanics and Biomedical Engineering*, 11(3):263-279 (2008).
[2] M. Teschner, B. Heidelberg, M. Muller, and M. Gross. A Versatile and Robust Model for Geometrically Complex Deformable Solids. In *Computer Graphics International* (CGI 2004). pp. 312-319 (2004).

Learning through exploration: a bird's eye view

Zoe Demery & Jackie Chappell
zxd878@bham.ac.uk
School of Biosciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

Introduction

- Research has focussed on ***what*** different species' cognitive capacities are, rather than ***how*** animals structure information, especially by **exploration**.
- We believe exploration is not random; but **structured, selective and sensitive** to particular categorical features of the environment[1,2].
- We have exploited the natural exploratory tendencies and unique sensorimotor apparatus of **parrots** to investigate the mechanisms of learning about object properties through **vision and manipulation**.

Key Questions

1. How do parrots' visual fields and bill tip organ support their exploratory learning?
2. What cues are parrots particularly sensitive to?
3. How does their exploration change with environmental changes?
4. What does this suggest about their internal folk physics?

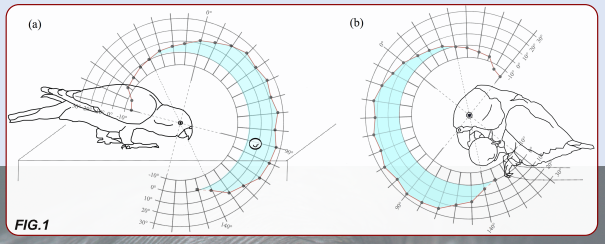


FIG.1

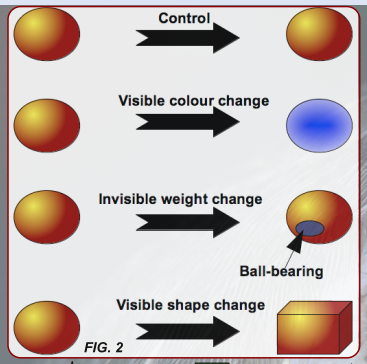
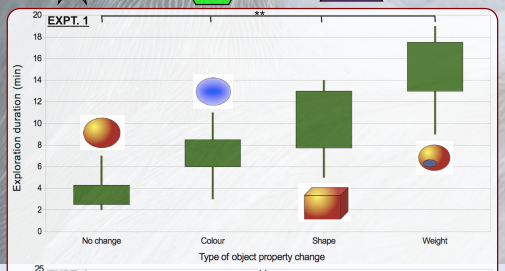


FIG. 2

Methods

- We measured Senegal parrot (*Poicephalus senegalus*) visual fields by the **ophthalmoscopic reflex technique** and studied touch receptors in their bill to characterise the limits of parrots' **cross-modal exploration**[3].
- This led to two behavioural experiments to look at the exploration process in detail, specifically kakarikis' (*Cyanoramphus novaezelandiae*) sensitivity to **functional invisible cues** (weight, centre-of-mass) versus visible cues (colour, shape)[FIG.2].
- Using a counterbalanced, repeated measures design, we consecutively presented 10 parrots individually with **rigid, novel objects of different shapes, colours, weight and centres-of-mass**.



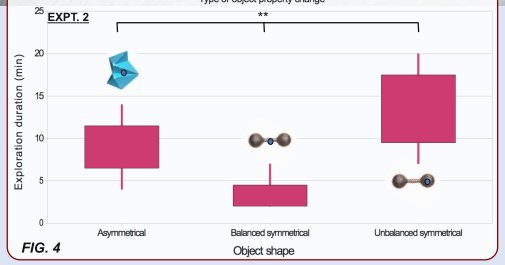


FIG. 4

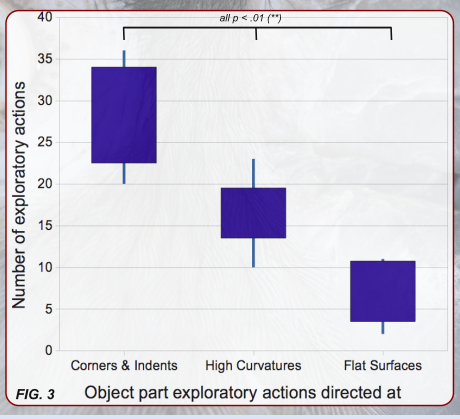


FIG. 3 Object part exploratory actions directed at

Conclusions

- Parrot visual fields are unlike those of any other birds, with both quite a **broad frontal binocular field** and nearly comprehensive view **around the head**[FIG.1].
- Perhaps the bill tip organ allows the visual field to **shift up & back** for better predator detection, so once grasped, object exploration seems to be largely haptic.
- **Corners/indents & highly curved edges across both behavioural experiments**[FIG.3] were explored more than flat surfaces.
- **Experiment 1:** an invisible weight change was explored more than a visible shape change, and even moreso than a less functional colour change[FIG.2,4].
- **Experiment 2:** an asymetrical shape was explored more than a symmetrical shape, unless the centre-of-mass was unusually on one side[FIG.4].
- **Novel, functional or unexpected environmental changes** seem to cause more exploration[FIG.4].

REFERENCES
[1] Demery, Z., Rios, V. E. A., Sloman, A., Wyatt, J., & Chappell, J. (2010). Construct to Understand: Learning through Exploration. In Proceedings of the International Symposium on AI-Inspired Biology (pp. 59–61). Presented at the *Proceedings of the International Symposium on AI-Inspired Biology*.
[2] Chappell, J., Demery, Z. P., Arriola-Rios, V., & Sloman, A. (in press). How to build an information gathering and processing system: lessons from naturally and artificially intelligent systems. *Behavioural Processes*.
[3] Demery, Z. P., Chappell, J., & Martin, G. R. (2011). Vision, touch and object manipulation in Senegal parrots *Poicephalus senegalus*. *Proceedings of the Royal Society B*, 1–8. doi:10.1098/rspb.2011.0374

How can children inform our understanding of exploratory learning in non-human animals?

Zoe Demery, Sarah Beck & Jackie Chappell
zxd878@bham.ac.uk
Schools of Biosciences & Psychology,
University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

BBSRC bioscience for the future

Introduction

- Piaget's view – that children learn through play and exploration – is widely accepted as being integral to cognitive development.
- Surprisingly few scientists have systematically investigated **how exploration is structured** to support learning mechanisms in different situations and even fewer have studied it in non-human animals.
- Traditionally, the methodological approach for studying cognitive development in human and non-human animals has been very different, but a **comparative approach** can be very informative.
- We exploited the strong explorative tendencies of **parrots and human children**, and designed a series of comparative experiments to provide a window into the mechanisms and strategies used in causal learning.

General Methods

- Here we focus on the human studies, where we presented **three increasingly complex tasks** involving novel objects and physical problems to school children.
- The children (**2-7yo**, *n*=106) were tested individually in a classroom setting, using a counterbalanced, repeated measures design, with controls for any side biases.
- In each task, we recorded their exploratory behaviour in detail and measured their total **exploration duration and number of different exploratory actions** upon each test apparatus.
- Each task examined different aspects of exploration and we asked whether these could form **exploration stages** in development.

Task 1: Categorical perception in exploration

- Are subtle **changes in invisible functional cues** (e.g. action, weight) for an object's properties attended to more than changes in **non-functional visible cues** (e.g. location, colour)? Is this attention even more pronounced for **unexpected, within-type than expected between-type** changes?
- ***Goal:*** get the ball out of the box[FIG.1].
- All children were habituated to **pushing a ball from the top** of box, then presented with one of four conditions.

Task 2: Physical rules in exploration

- Do individuals use **physical rules** (e.g. solid objects can't pass through each other) or **habituated action sequences** (e.g. with trial-and-error learning) to direct their exploration?
- ***Goal:*** get the lego men out of the tube[FIG.2].
- Habituated to apparatus without **obstructing block**, then presented with block.

Task 3: Causal inferences & abstraction in exploration

- Do individuals use **knowledge about hidden items** to direct their exploration?
- ***Goal:*** get one of the marbles out of the box[FIG.3].
- The children could use the **plungers** to act on the marbles, but there was a hole in only one of the halves of the box. In the later trials, different halves were **covered** up.

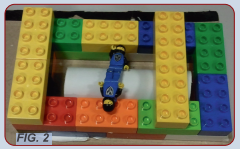


FIG. 2

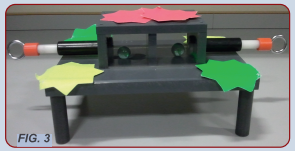


FIG. 3

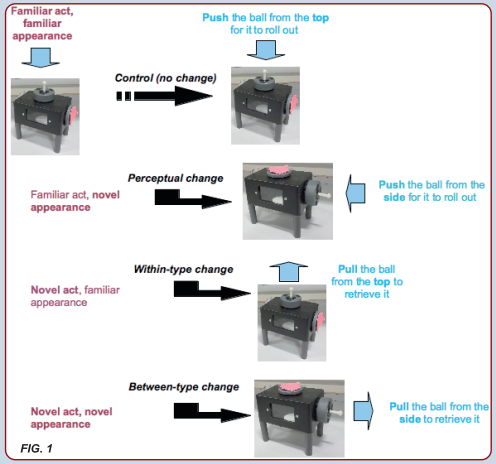


FIG. 1

General Key Questions

1. Does **exploration time** change with age?
2. Doe the **diversity** of exploratory actions change with age?
3. Is there greater causal **understanding and success** at solving tasks with age?
4. Does the **frequency and sequence** of exploratory actions change with age?

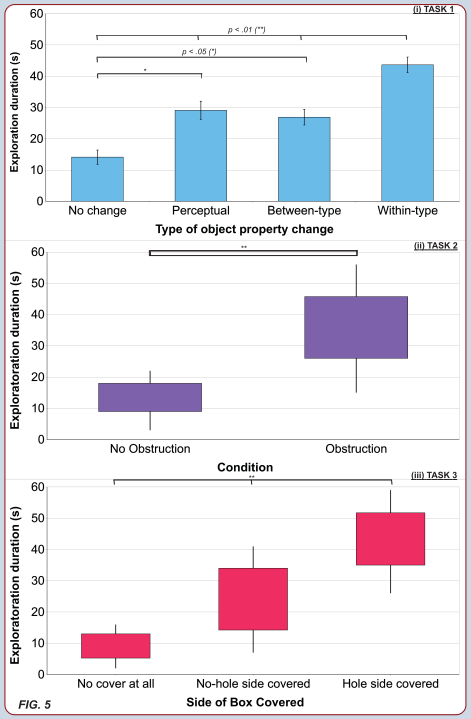


FIG. 5

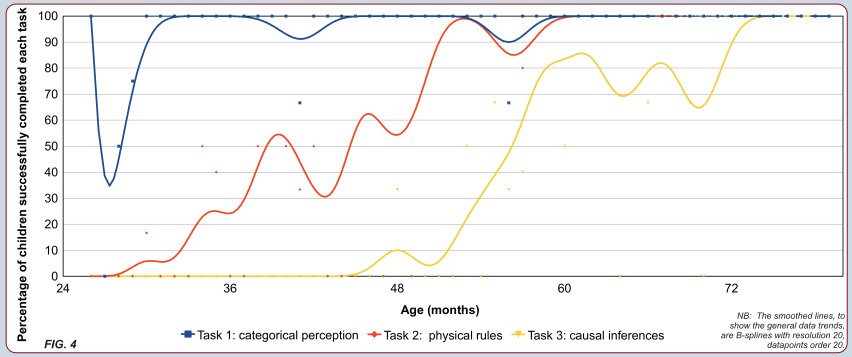


FIG. 4


FIG. 6

Conclusions

- The three aspects of exploration we tested seem to **occur consecutively** in development[FIG.4].
- **Task 1:** children **explore more when there are invisible functional changes** in an object (especially **within** an object type), but all visible cues are still attended to[FIG.5(i)]. Also the diversity of actions increases with age when functional changes occur.
- **Task 2:** children explore more when a solid obstruction is introduced[FIG.5(ii)] and **increasingly touch the obstruction first with age**, rather than follow through the habituated action sequence[FIG.4].
- **Task 3:** children seem to use previous knowledge, and **explore more when objects are hidden**[FIG.5(iii)]. Older children can make causal inferences successfully[FIG.4].
- These results are reflected to some extent in comparative tests with parrots (*Cyanoramphus novaezelandiae*[FIG.6]), which face **similar ecological problems** to us.
- We hope this will give us insight into how we and other animals process information in a wide range of environmental situations.

APPENDIX B

Calculations for object position in visual field on approach

For more information on the experiments these calculations relate to, see chapter 3 and chapter 4.

These calculations make the following assumptions:

- Take a top-down, two-dimensional view of the bird in relation to the object along the x, y-axes, so discount any head movements along the z-axis for instance;
- Assume the bird always orientates its head to focus on the item of interest in the plane/elevation of maximum binocularity, which happens to be at elevation 90º (Figure 2.3.1d);
- Assume that the eye is looking in the 'average direction', but there will an error of ± 20º due to eye movement.

Given the reference points shown in figure Figure B.0.1, the distance (d) and

angle (θ) of the object from the bird is readily found to be:

$$d = \sqrt{(x_n - x_2)^2 + (y_n - y_2)^2}, \tag{B.0.1}$$

$$\theta = \tan^{-1}\left[\frac{y_2 - y_1}{x_2 - x_1}\right] - \tan^{-1}\left[\frac{y_n - y_2}{x_n - x_2}\right]. \tag{B.0.2}$$

The only additional care that needs to be taken when calculating the angle is that if the true angle falls outside the primary range of $\tan^{-1}$, then an appropriate multiple of 180^o must be added to correct this.

From this we can calculate which portion of the visual field the object is in at any given moment:

- if the angle of the object, θ, is less than the angle associated with the binocular field (13.5^o), then the object is in the bird's binocular filed of view;
- if it is greater than this angle, but still less than the angle of its maximum field of view (172.5^o), then the object is in the bird's monocular field of view (right monocular field if positive; left if negative);
- an angle larger than this indicates that the bird cannot see the object at all.

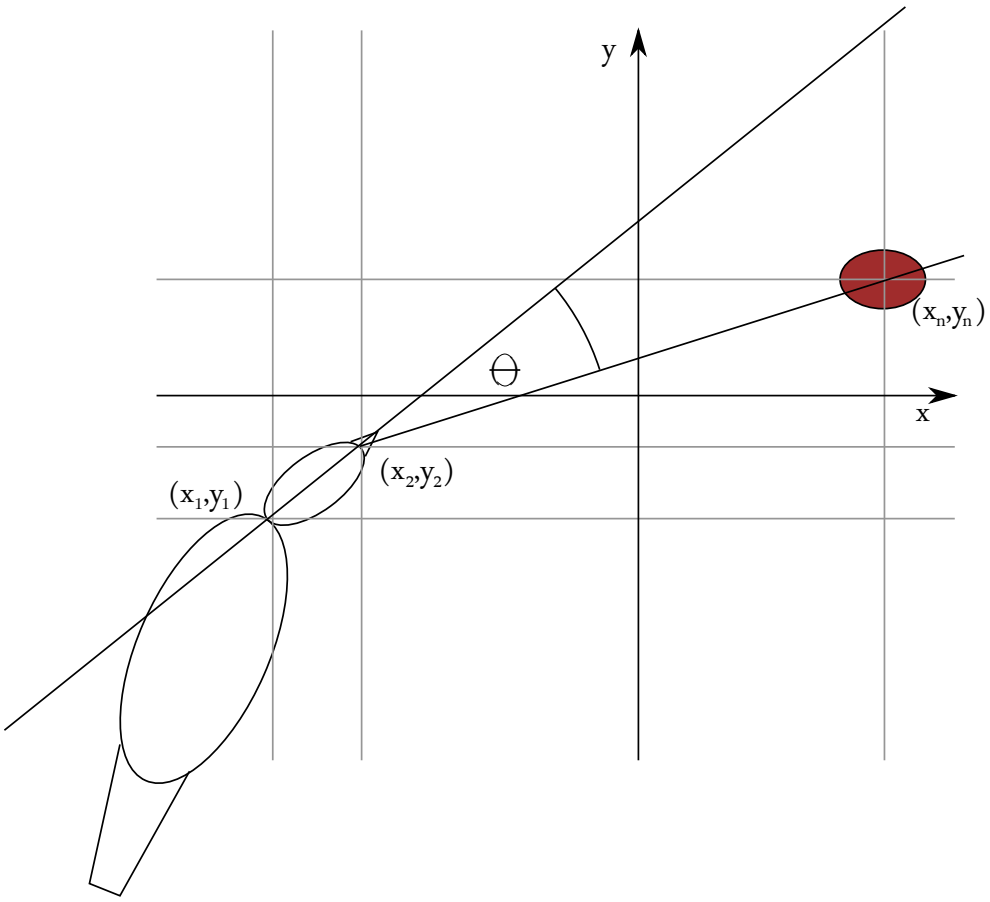


Figure B.0.1 – Diagram illustrating the approach of a bird to a target object, with the three locations that were measured and tracked in time labelled. These locations are relevant for calculating where the object was in the visual field. The object is at (x_n, y_n), the mid-point between the eyes is at (x_2, y_2) and the rear of the bird's head is located at (x_1, x_2).

APPENDIX C

Exploratory and non-exploratory ethograms

Table C.1 – An ethogram of the exploratory behaviours exhibited by the kakariki (*Cyanoramphus novaezelandiae*) and human children. This was of particular interest in chapter 6 on page 159 and chapter 7 on page 225 (but also relevant in chapter 4 on page 63; and chapter 5 on page 119). These categories were based on preliminary observations of the kakariki in their home cages and previous animal object manipulation studies (Collar, 1997; Diamond and Bond, 1999; Bard, 1995; Power, 2000; Hayashi and Takeshita, 2006). Each exploratory behaviour category was assigned one of three levels of complexity (1. simple; 2. intermediate; 3. complex), according to how cognitively and physically difficult it was for the individual to perform the behaviour. Complexity was greater when a behavioural category required multiple appendages, and/or became focussed on multiple objects or object parts. The 'codes' or characters/symbols in brackets refer to the keyboard keys associated with each behavioural category. They were recorded using JWatcher (Blumstein et al., 2007). For each of the exploratory behavioural categories, a note will be made of which appendage the object is in, as well as which part of the object it is focussed on (e.g. corner/surface) and what it is targeted at (e.g. another object/own body part/another individual) (Table C.3). Note that 'prolonged grasping' behaviours generally lasted more than 3 seconds, whereas 'transitory grasping' behaviours lasted less than 3 seconds.

Category		Code	Sub-category	Level of complexity	Description
Visual Inspection (;)		l	Look	1	Visually investigating static object(s)/body part with head either still or turning around the item of interest.
		f	Follow	2	Locomote after a moving object, but without touching it and just watching its movements.
		m	Move into visual field	3	One of the appendages while grasping the object will move it into the individual's midline axis of the binocular field, or up close to one of the eyes.
		s	Search	3	Locomote and turn head for out-of-sight object.
Grasping (J)	Transitory ([)	M	Mouth	1	A forceps- like movement of the bill (opposing the tips of the mandible and maxilla) or mouth often accompanied by in-and-out movements of the tongue.
		t	Tap	1	Briefly touched with an appendage, maybe in a clawing-like motion with one of the feet/fingers. No actual permanent holding.
		p	Probe	2	Into an object with an appendage. May drag appendage along crevice.
	Prolonged (])	h	Hold	1	Static holding of an object. Can occur in conjunction with a manipulation of some kind in another appendage.
		c	Carry	1	Holding with locomotion. Object is transported to another location by running, walking, climbing or flying (note type etc.).
		R	Releasing	1	Dropping object, not due to another agent acting on the object or subject.
		T	Transferring	2	Passing the object from one appendage to another.
		H	Hold down	3	Stabilise object on a solid surface with an appendage. Can be manipulated in some other way with another appendage.

Category	Code	Sub-category	Level of complexity	Description
Actions (“)	P	Push	1	/press, perhaps with kicking motion. Can 1 object into another. Note if attempted (force obviously applied but not successful in moving object). Not going to pick up on all the instances.
	q	Pull	1	Can be using one object to retrieve another on top of it. Like ’Push’, note if attempted and force applied.
	r	Rotate	2	Rotate and twist object, often with neck. Can be in relation to another, such as to put through a gap. Note if object instead rotated by flipping the edge of the object.
	S	Shake	2	/swing around
	e	Translate	2	Slide an object along or on top of another (note) by constant contact with object and so not a simple pushing motion.
	u	Throw	3	While an object is held in an appendage (often beak), it is let go with a quick lateral or vertical movement of the neck, so that the object is flung for some distance through the air. May be accompanied by a hop or wing flap.
	d	Catch	3	Note if attempted or successful.
Modifying objects (/)	b	Bend	1	Move 1 part in relation to another part of the object, which is of flexible or pliable material.
	Q	Squeeze	2	Compress object to change the shape of it, especially when acted upon a soft, yielding material.
	W	Hit	2	Repeated forceful action to substrate/self (note).
	I	Pry	3	Usually using the beak as a lever, the tip catches a crevice and the maxilla is pulled & twisted to open up object sides – exerted mainly from head & neck.
	a	Pull apart	3	Break object into pieces by holding down with foot & pulling away w/ beak.
	C	Scrape	3	Claws or mandibles forcefully moved up & down against object to try to move bits off its surface in scraping action

Category	Code	Sub-category	Level of complexity	Description
Relating objects (?)	x	Extract	3	One from inside another using appendage
	i	Insert	3	Put one object inside another
	L	Pile	3	Put or wad objects together, either side by side or on top of one another.
	k	Hook	3	Use one object as a hook to retrieve another by pulling.
	A	Arrange	3	Sort several objects in some way e.g. line up or to remove an object as an obstacle to another. Note type.
	D	Drape	3	Hang or wrap one flexible object over or around a more solid one

Table C.2 – An ethogram of the non-exploratory behaviours exhibited by the kakariki (*Cyanoramphus novaezelandiae*), which was of particular interest in the home cage (chapter 5 on page 119), but also relevant during the cognitive tests (chapter 4 on page 63; and chapter 6 on page 159). These categories were based on preliminary observations of the kakariki in their home cages and field studies (Greene, 1988; Collar, 1997; Diamond and Bond, 1999; Kearvell et al., 2002). The 'codes' or letters in brackets refer to the keyboard keys associated with each behavioural category. They were recorded using JWatcher (Blumstein et al., 2007).

Category	**Code**	**Sub-category**	**Description**
Locomotion (L)	W	Walking	A slow gait locomoting around the area, but not while exploring object(s).
	R	Running	A fast gait locomoting around the area, but not during exploration.
	F	Flying	Flapping wings
	C	Climb	Up side of cage, with pulling-up motion of beak, followed by claws.
	H	Hopping	Jumping action on one leg.
	O	Other	e.g. rotational, somersaults, jumping
Posture (P)	O	Eyes open	Not observing object or other, but sitting or standing still with eyes open and alert.
	L	Single leg	Standing on one leg.
	T	Head tucked	Under wing or on back.
	C	Eyes closed	Eyes closed
Maintenance (M)	D	Defecating	or urinating
	P	Preen	Clean own feathers with beak or scratch
	I	Ingestion	Ingest food or drink
Social (S)	V	Vocalise	
	P	Allopreen	
	C	Courtship behaviour	Including mating and feeding another.
	A	Agnostic	
	C	Conciliatory	
	R	Social roosting	
Other (O) Miscellaneous behaviour			

Table C.3 – Details of the JWatcher modifiers and their respective keyboard keys ('codes'). Each exploratory behavioural category (Table C.1) often had a 'modifier' associated with it, such as what appendage was holding the object. See Blumstein et al. (2007, p. 30) for more information.

Modifier Group	**Modifiers**	**Codes**
Focussed object part	surface	%
	edge	$
	corner	^
	obscured side	+
	inside	&
Appendage	bill/mouth	8
	left foot/hand	9
	right foot/hand	0
	other (body/wing)	-
Target	object(s)	!
	self (body part)	@
	another individual	£

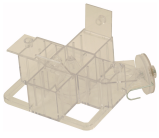
APPENDIX D

Environmental enrichment toys

Table D.1 – The name, image and description of the environmental enrichment toys in the 'unenriched' housing conditions (chapter 5 on page 119). They were all sourced from Northern Parrots (Ramsbottom, UK). The unenriched toys were not rotated between the cages on, but their position within the cage did change weekly. They were called 'simple toys', as they afforded simpler behaviours than the complex toys (Table D.2), such as basic climbing or manipulation opportunities. Theoretically all the behaviours described in Table C.1 could be performed on all of the toys.

Image of Toy	Name of Toy	Description
	Talk 'n' Play	Four buttons that could be pressed to play different sounds.
	Silo Mammoth	Knotted ropes and wooden blocked that could be chewed and climbed upon. Each block had a bell attached to the end of it.
	Figure-of-eight rope	A rope in a figure of eight shape that could be used for climbing/swinging upon or chewing. A tennis ball was on one end of the rope.
	Mop-head	A mass of string attached to a hard plastic end, which could be chewed and pulled apart.

Table D.2 – The name, image and description of the environmental enrichment toys in the 'enriched' housing conditions (chapter 5). They were all sourced from Northern Parrots (Ramsbottom, UK). The enriched toys were rotated between the three enriched cages on a weekly basis. They were termed as 'complex toys', as they were designed to to stimulate problem-solving abilities or causal understanding (versus simple toys in Table D.1). Theoretically, all the behaviours described in Table C.1 could be performed on all of the toys.

Image of Toy	Name of Toy	Description
	Crazy 8's	Food items could be placed in the top of the toy, which then falls down inside the roy. To retrieve the food item, the whole toy must be rotated.
	Treasure Chest	Differently shaped wooden blocks and food items could be placed inside the chest. They could be retrieved through the appropriately shaped holes in the side of the toy.
	Snack Rack	Each level of the toy could be individually rotated to reveal food, which means there were several difficulty levels.
	Parrot's Treasure	The keys could both be turned to remove the bottom of the toy, to allow an embedded food item to fall out.
	Foraging Wheel	The inside of the toy could be rotated to move the inner compartments and retrieve the embedded food within each compartment.
	Gear Head	Handles on the outside of the toy could be moved to turn the two cogs on the inside.
	Jumbo Nut 'n' Bolt	The plastic nut and bolt could be taken apart and put back together.
	Foraging Carousel	Four compartments on a rotating base. Each compartment could be opened in different ways (e.g. twist cover/drawer).
	Hanging Puzzle Tower	The food item could be inserted in the toy, but then it could only be retrieved by pulling out each level of the 'tower'.

APPENDIX E

'RoboBella'

A selection of 'built-in properties' that a 'virtual parrot' may have, as mentioned in chapter 8, which has been shown to work in a very basic simulated environment using StarLogo TNG version 1.5 (Colella et al., 2001). Follows work from Arriola-Rios et al. (2013), where we hoped to apply the artificial model described therein to a range of materials and problem-solving tasks. To check the ecological validity of this artificial model, it should be verified against a wider range of biological examples, under different experimental conditions (as in chapter 6).

Table E.1 – Programmed rules that make up a 'virtual parrot'. The two main senses of exploration are visual and haptic. The key set of rules for visual exploration was the locomotion and approach parameters. The key set of rules for haptic exploration was dependent on the properties of the object collided with, perform certain actions. The stages refer to the Three-stage Theory of Exploration described in Demery et al. (2010); Arriola-Rios et al. (2013).

Stage	Rule
1	Move and turn around in environment randomly, bouncing off edges of environment and turning in opposite direction.
1	If move within 50 cm (or collided with) with an object, then approach it. Preference for object in front within visual field.
1	Avoid objects explored previously, and explored object types have exponential disinterest
1	Explore novel objects more than familiar objects
1	Explore corners more than surfaces
1	Explore high curvature more than low curvature
1	Explore compliant objects more than rigid objects
2	Explore shape and texture more than colour and stripy patterns
2	Perform specific selection of actions on specific object types, but randomly performing a different action every other exploration bout. Each action provides information about a specific object property.
2	If weight and balance contradicts observed shape, explore more
2	Any changes in the above object properties from what was previously explored, results in greater exploration
3	When quality of explored evidence below certain threshold, explore for longer than usual

APPENDIX F

The Three-stage Theory of Exploration

The Three-stage Theory of Exploration

Zoe P. Demery and Jackie Chappell

Centre for Ornithology, School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

Abstract

Faced with a vast, dynamic environment, some animals and robots often need to acquire and segregate information about objects. The form of their internal representation depends on how the information is utilised. Sometimes it should be compressed and abstracted from the original, often complex, sensory information, so it can be efficiently stored and manipulated, for deriving interpretations, causal relationships, functions or affordances. We discuss how salient features of objects can be used to generate compact representations, later allow- ing for relatively accurate reconstructions and reasoning. Particular moments in the course of an object-related process can be selected and stored as 'key frames'. Specifically, we consider the problem of representing and reasoning about a de- formable object from the viewpoint of both an artificial and a natural agent.

Keywords: Learning, Animal Cognition, Representations, Deformable Objects

Material from of this paper has formed part of three publications (Demery et al., 2010; Chappell et al., 2012; Arriola-Rios et al., 2012).

1. Introduction

The brain of any animal is finite, so it cannot contain a perfect model of the world around it. Animals receive a variety of information through their sensors, but how useful that information is dependent on several factors including: environmental conditions; the accuracy of information processing and interpretation; the information's use; and the animal's behavioural response (Sloman, 2011). An individual must balance the amount of useful, relevant information obtained about its surroundings against the energy expended in gaining it (Chappell and Sloman, 2007). What is unclear is which bits of information are most useful for processing and storing in the brain, or how they can best be represented. Principally, we propose that when an individual gathers information through its senses, it often forms object representations supported by systematic exploration[1].

Exploration is found throughout the animal kingdom and environmental contexts (e.g. Berlyne, 1960; Glickman and Sroges, 1966). Yet to date, there has been little systematic, quantitative research about it, and its structure in supporting learning mechanisms of different individuals (for more discussion see White, 1959; Rochat, 2001). What research there is, has largely originated from the field of developmental psychology (chapter 1). Here it is widely accepted that exploration is integral to a child's learning and causal understanding about their world. However, many developmental psychologists advocate probabilistic learning as

Email address: zoe@vortices.com (Zoe P. Demery and Jackie Chappell)

[1] Cognition does not always rely on internal representations and the degree of detail in any internal representation can vary greatly depending on the situation. Quite complex-looking actions can often be performed by simple mechanisms and small neural architectures (e.g. Webb, 2001; McCrone, 2006). For instance, there can be a lack of detail especially when the environment can largely control an animal's behaviour, such as in flocking behaviour or in using pheromone trails. Here alternative, but complementary, mechanisms may be more relevant, such as emergency or embodiment (reviewed in Calvo et al., 2008). However, in this chapter we will not consider these cases and are concerned with more complex, cognitively flexible animals.

the sole mechanism to explain human exploration, contending it cannot be extended to other animals (Schulz and Sommerville, 2006; Schulz and Bonawitz, 2007).

Among the non-human animal researchers, behavioural ecologists view exploration as another instinctive motivation, like foraging or courtship, driven by uncertainty in variable environments (e.g. Miller and Dollard, 1941; Inglis, 1983; chapter 1). The moves towards integrating cognitive processes (e.g. discrepancy reductions or spatial cognitive maps), are discussed in the context of passive animals driven by impulses, rather than conscious individuals, reasoning about the world around them (Toates, 1983; Loewenstein, 1994; Inglis and Langton, 2006). Taking an evolutionary perspective, this field pays slighter attention to the individual's perspective.

Animal cognition researchers have focussed on what the different cognitive capacities of different species are, rather than how they process information to achieve those capacities (Shettleworth, 1993; Thomas, 1996; chapter 1). For example, the 'trap-tube task' is a typical litmus test for causal understanding of gravity, which has revealed much about various species (e.g. Visalberghi and Tomasello, 1998; Penn et al., 2008; Taylor et al., 2009). This test is only a binary measure, however, of whether an individual can complete the task – not what the underlying processes are.

An under-represented approach is the structural-mechanistic model (chapter 1). The aim here is gain answers by studying the pattern or sequence of exploratory behaviour (e.g. Gibson, 1988; Renner, 1990; Sloman, 2008a; Magnani, 2009). The sensorimotor apparatus of an exploring animal is considered, asking how the senses support exploratory learning (e.g. Gibson, 1962; Mesulam, 1998; Shams and Seitz, 2008; Demery et al., 2011).

This perception-orientated approach is a blossoming area particularly in artificial intelligence. Designing such cognitive models requires specific parameters, which can aid animal behaviourists to form concrete, testable hypotheses (for more information see Demery et al., 2010). However, it seems there is not yet a robot/simulation that can form concepts, or generalise information to new situations like some animals. Cognitive roboticists have looked at different learning mechanisms in isolation with relative success, but few projects have tried combining them into one information-processing system (e.g. Hawes et al., 2010; Markram, 2006; Timmis et al., 2008).

In Part I of this thesis we investigated how the senses can support information-gathering by exploration. In Part II we considered how the environment can influence exploration. Now we will start to consider how such an information-processing system is built. In this chapter, inspired by the designer-based approach used in artificial intelligence, we will take a distinctive top-down perspective. We will first examine some of the general environmental features that make it easier for animals to internalise the surrounding world and make predictions about it, but also some environmental problems that need to be overcome (Section 2). From this, we will consider how these features may be processed by the design of the animal's exploratory system. We integrate elements from each discipline discussed above in a novel way, leading to our Three-stage Theory of Exploration.

We propose that when forming representations, object exploration is not always random, but *structured*, *selective* and *sensitive* to particular features and salient categorical stimuli in the environment. Further, an exploring individual can follow through three stages of theory formation – the forming (Section 3), the testing (Section 4) and the refining of hypotheses (Section 5). Each hypothesis is probably specific to a particular group ('exploration domain') of processes or affordances, but they may also be generalisable to novel contexts. We will lastly consider how we may test this theory, particularly through a series of comparative behavioural tests on parrots and humans (Section 6) – both being notoriously exploratory and playful throughout their lives (chapters 6 and 7).

2. Predictable environmental features

As a basis for the Three-Stage Theory of Exploration, we first consider what features in the environment are reliably constant enough for an individual to learn about them. Shaw (2008, page 5) suggests,

> "The chief end of an intelligent individual is to understand the world around it."

The word 'understanding' implies the animal can make predictions about the world. For this, the animal needs to be able to detect salient features in its environmental niche. It can do this by actively exploring its surrounding environment, often by combining perception and cognitive analysis with action. An exploring animal is driven by its goals. These can be explicit goals, such as foraging or particular problem-solving tasks. Alternatively, they can be implicit goals, such as gathering information by apparently random playful or exploratory behaviour.

Some of the environmental features perceived and learned about may come with environmental problems; these problems must be surmounted first. No two animals face the same environmental problems, as the specific features perceived depend on the life history strategy of each individual, as well as the affordances of each individual's niche (Greenberg and Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002). The following subsections present a general list of environmental features and problems, which may be perceived and solved by various exploratory species (see also Chappell et al., 2012).

2.1. Persistency

For an animal to make relatively accurate environmental predictions, a few unchanging features need to persist in the environment for a significant length of time. The information-processing system should assume these properties continue to exist in a range of environmental contexts, which differ in space and time. These features can then be utilised by the animal's learning mechanisms, to develop a representation of the world.

We expect all individuals to work from the assumption the environment is persistent (enabling them to re-use information), but the strength of this persistency-assumption will vary across species. The parasitoid wasp (*Ammophila dysmica*) displays a sophisticated-looking behaviour sequence (Fabre et al., 1918; Rosenheim, 1987), which is in fact genetically fixed. Any small change to the environment renders the wasp confused and behaving erratically, as it works from the assumption of universal persistency. Rats (*Rattus norvegicus*) in a maze are not confused by changes to layout (e.g. Wilz and Bolton, 1971; Albert and Mah, 1972), as their assumptions of persistency are flexible enough to cope with these changes.

2.2. Regularity

Environmental regularity is the predictable presence of certain features, which can be learned by an animal perceiving a fixed relationship between occurrences[2]. These environmental patterns enable partial representations, particularly when an individual is faced with different causal problems. Causality is a type of regularity, where partaking elements are not always identifiable, but whose manifestation always entails the same consequence.

Animals should have mechanisms capable of detecting and exploiting these patterns. It is likely they categorise the environment, selecting key features linked by predictive relationships[3]. Among the mechanisms capable of detecting such patterns is 'associative learning', which has been studied extensively in several species Shettleworth (for a review of the different mechanisms see 1999). For example, information about food availability will become associated with the act of feeding, so the presence of this information will increase foraging activity. Even very simple animals (e.g. nudibranch, *Hermissenda crassicornis*; Alkon et al., 1982) can detect causal associations and patterns in time and space.

2.2.1. Sequentiality

Sequentiality is a series of features, nearly always perceived in the same order[4]. The first few features can be used to identify the sequence and predict either the following features, or the rules-set needed to process them. Examples include lightning flashes being followed by thunder claps, or listening to the sound of a prey and preparing to chase.

[2] Regular environmental features can be present as groups of features, in different dimensions, or in a hierarchical structure.

[3] The information contained within each of these discrete categories can include information about continuous features (e.g. length/height).

[4] These may not be contiguous and can include cause-and-effect learning.

2.2.2. *Branching sub-sequences*

Further to sequentiality, there can be a succession of sub-sequences. The links here would allow a few options to follow, such as beginnings of other sub-sequences. This forms a branching structure, which becomes layered, modular, and sometimes hierarchical (e.g. Arriola-Rios and Savage, 2007). This branching structure found in the environment, may be reflected in an animal's internal representation (see also Section 4).

The maximum length of a sequence, and the maximum number of branches that can be remembered and manipulated, impose strict limitations upon what the individual can understand, and the types of patterns it is capable of detecting. However, this branching structure would allow more complex individuals to make abstractions. Concepts formed at one stage could be re-used and refined to repeatedly form ever more complex concepts in multiple ways (see Section 5). This allows for progressively specific and parallel processes, such as the models described in Karmiloff-Smith, 1995 (subsection 3.2). For example, the New Caledonian crow (*Corvus moneduloides*) has been shown be particular adept at detecting and planning through multiple-steps in a environmental sequence (Wimpenny et al., 2009). Although the end result was a complex display, the constituent steps could be simple mechanisms.

2.3. *Consistency*

When multiple mechanisms are used to collect and process sensory signals, sometimes they complement each other, by providing different information about the same object of interest. This may provide superfluous information, but it also allows the animal to confirm its own sensory inputs and establish the information is reliable. It is important for the animal that different mechanisms of perceiving or deducing the same thing are consistent with each other. For instance, an individual exploring a potential food item, should receive tactile information in agreement with the position and surface it sees.

2.4. *Redundancy*

Given the inherent limitations of the brain, animals can only build partial internal representations of their surroundings. These partial representations may not allow individuals to make perfect predictions for all environmental events[5]. As individuals receive sensory information, they may not succeed at processing relevant, useful[6] signals. Therefore, we expect there to be errors at different levels of the perceptual and cognitive processes. Thus, information-processing systems should be built in such a way as to tolerate this margin-of-error.

Some animals have more than one mechanism to perform actions, find things, or solve problems. The individual could just use reactive mechanisms, dependent on different layers of sensory-signal filtering, or it could use a combination of different learning mechanisms. While qualitatively different, all of these mechanisms produce similar, valid results, which overcome the problem of environmental redundancy. What is not clear is how each of these mechanisms allows the animal to learn about and retain only the relevant information. How does the animal reconstruct faulty perceptions from new perceptions that convey the same information?

For example, Horner and Whiten (2005) presented a puzzle box to chimpanzees (*Pan troglodytes*) and human children. The puzzle box was designed so that there were different ways of getting into it, although all the ways led to the same result (retrieving the reward out of the box). Children tended to directly imitate, action for action, a demonstrator's way of getting into the box. This included the irrelevant actions, which did not actually help them attain the goal. However, the chimpanzees did not imitate the demonstrator, but *emulated* them. In other words, they only performed their own relevant, functional actions to attain goal. These issues will be discussed below in subsection 2.6.

2.5. *Variability*

Many environments vary over time; due to changes in climate, geology, competitors' behaviours, co-evolutionary arms races between predators and prey, niche construction (e.g. Sterelny,

[5] An animal (e.g. a nematode, *Caenorhabditis elegans*, or even various forms of bacteria; Qin and Wheeler, 2007; Ben-Jacob, 2009) in a very simple environment can make perfect predictions; but we are not concerned with these cases .

[6] Here, relevant or useful information is that which – if acted on – will influence the animal's evolutionary fitness.

2007) and food availability (e.g. Houston et al., 1980; Kacelnik and Krebs, 1985; Kacelnik and Todd, 1992). Little experience is needed in a relatively static environment, where precocial animals – whose behaviour has been almost completely determined by their genome – just need to survive long enough to reproduce (e.g. wasp described in subsection 2.1). Other individuals are required to adapt to diverse, dynamic environments by learning (for greater discussion see Chappell and Sloman, 2007; also see chapter 5).

The different exploratory mechanisms, for extracting relevant information (subsection 2.4), are likely shaped by experience. The animal should seek out information to reinforce, evolve and, where possible, prove or disprove its current internal representations, particularly if its expectations are violated. Depending on the individual's needs and competences, a specific, relevant subset of experiences allow specific, relevant features of its niche to be captured (e.g. von Bayern et al., 2009). We believe there is continual extension of these 'branches', or 'information blocks', throughout the individual's life. At different developmental stages, a human child likely takes in different aspects of the same overheard conversation, or different aspects of the operation of the same tool, then later adapts accordingly (see discussion in Sloman, 2010).

The kea (*Nestor notabilis*), a New Zealand parrot, has proved very adaptable and cognitively flexible. Huber, Gajdon and colleagues (reviewed in 2006) have documented how kea display quite innovative behaviours in relatively artificial situations, such as lifting restaurant bin lids through various steps. Kea have been shown to learn from previous experiences, even from several months ago. They also seem very exploratory during problem-solving, although there are several individual differences in strategies employed (e.g. Auersperg et al., 2011).

2.6. The cyclical animal-environment interaction

Together these environmental features and problems form a structured universe (Section 2). Parts of this structure can be perceived and understood by animals. The existence of these predictable features reduces the amount of information needed to represent the environment. Once the animal has processed sufficient features, the remaining important information can be inferred when needed – the question is how.

There is increasing evidence (at least in humans, e.g. Gibson, 1988; Cook et al., 2011) that exploration is not random, but structured, selective and sensitive to particular environmental stimuli. We propose exploration is composed of structured behavioural strategies supported by specific sensorimotor predispositions (e.g. see chapter 2). Thus, we turn our discussion to what internal features an exploratory animal may have to process environmental information. In parallel, we consider how these internal features may manifest themselves on the external world via the animal's exploratory behaviour (Section 6).

Although many of these features have been studied before in isolation, no one has yet integrated them into one information-processing system, or addressed the short-comings of each type of mechanism (chapter 1). Additionally, no one has comprehensively considered how they may follow on from one another over a lifetime. We propose that exploratory animals, from the start to the end of their lives, generally follow three stages of exploration. How they progress from one stage to another may vary between exploration domains (and between individuals) and there may be some overlap between the stages. The actual time-scales for each stage's progression are not clear and are ripe for future research (Section 6). In the first stage, an individual forms their hypotheses about the world (Section 3), then they test these hypotheses in the second stage Section 4. The final stage is the individual extending and refining their hypotheses (Section 5). There are different design features within each stage, discussed below.

3. Stage I: forming hypotheses

We propose in the first stage the animal forms hypotheses about the world by interacting with it. The individual is probably young and just beginning to gather information about the world around it. Consequently, it detects pattern in the environment using simple learning mechanisms, such as probabilistic learning, or trial-and-error (subsection 3.3). These are directed by sensorimotor predispositions (subsection 3.1), which are particularly sensitive to categorical stimuli (subsec-

tion 3.2). Their exploratory behaviour focusses on novel stimuli (subsection 3.5), or any obvious changes that are detected in the environment (subsection 3.4). We will now discuss each of these internal design features of Stage I separately.

3.1. Sensorimotor predispositions

A cognitive system consists of a body with a sensory and a motor apparatus that allows for interaction with the environment and a brain to map sensory stimulation onto motor actions (Floreano and Mattiussi, 2008). Merleau-Ponty (2002) was among the first to point out that the perceiver's physical body affects sensation; that perception is not simply a passive recording of environmental stimulation. The senses provide another level of *active* exploration, in addition to what is gained from physical body movement (chapter 3). Objects are invariable in the environment without movement/processes. For instance, bees can only see static snapshots of the world, so they generate their own processes by moving through it – thus perceiving through optic flow (Srinivasan and Gregory, 1992; Loomis and Beall, 1998)

The Gibsons (Gibson, 1977; Gibson, 1988) argued the infant's sensory and perceptual systems have evolved to pick up information that is already available in the environment, so no cognitive reconstruction of information needs to take place. The infant's perception detects invariant information (like that described in subsection 2.2) by differentiation across several experiences. They argued against traditional associative learning mechanisms: the infant is learning a richer series of different levels of signal quality of the same stimuli, rather than binary pairs of associations.

Certainly, it is helpful to look at what the environment offers, then consider how the organism is processing that information (as in Section 2). The environment offers regularities and invariant information, but as these still need to be sorted from the 'noise' (subsection 2.4), we should not discount construction of internal representations altogether. However varied the environments, certain competences will be hard-wired into the genes. It may be more efficient for the individual's brain to store information gathered from its different senses *amodally*, and group it into categories (subsection 3.2), perhaps in some sort of symbolic (rather than probabilistic), hierarchical structure (subsection 2.2.2).

It follows reason that an individual's sensorimotor system is adapted to attend to particularly important information, such as regularities providing information about different objects' affordances. Initial sensorimotor competences should be designed to make use of relevant environmental information, such as salient shapes with their: texture, edges/contours, curvatures and orientations of surface fragments. Object areas such as flat, smooth surfaces are less likely to contain useful information about the object, so more sensorimotor attention should be paid to corners, or areas of high curvature.

Some object properties are difficult to determine without touching them. For example, to determine weight, an individual needs to lift the object (Flanagan and Wing, 1997; Wing and Lederman, 1998). Information gained by haptic exploration does not need to be metrical. The exact properties attended to will depend on what sensorimotor apparatus the animal is equipped with, and on which features of objects or events are relevant to its ecological niche (e.g. psittacine visual fields and bill tip organ described in Part 1).

3.2. Object categorisation

To deal with the computational load of processing a dynamic environment (subsection 2.5), with a large amount of potentially redundant information (subsection 2.4), sometimes the animal may pursue a strategy of exploring the environment first, and then switching to exploiting it (e.g. Krebs et al., 1978). However, when other sources of uncertainty are involved, a learning system needs to also have good criteria for selecting environmental features to attend to.

Categorisation enables generalisation in novel conditions from a few experiences, while greatly reducing the computational complexity of perceiving objects and environmental processes. An enormously varied environment can be decomposed collections of object affordances and processes – i.e. exploration domains ('micro-domains' in Karmiloff-Smith, 1995). We suggest decomposition is achieved during exploration by perceptual and motor interactions with the environment (subsection 3.4). By concentrating on environmental

subsets and systematically varying its exploratory behaviour on it, the animal resolves what to attend to and limits the phenomena for which patterns are sought. As a prerequisite, the animal must start with perceptual mechanisms capable of detecting and recording the structures and motions produced by exploratory behaviours (subsection 3.1).

There have been many studies into what different animals can discriminate between (e.g. Kelman et al., 2008; Giret et al., 2009; Wills et al., 2009; Avargues-Weber et al., 2010; Soto and Wasserman, 2012; Wasserman et al., 2012). Pigeons can even tell the difference between art movements, something beyond many humans (Watanabe et al., 1995). However, they are likely rooted in quite simple same/different mechanisms, such as by differentiating between the variability in perceived thresholds of pairs of stimuli (Wright and Katz, 2006; Vermeulen et al., 2009; Wasserman and Young, 2010; Smith et al., 2011).

Alternatively, each object type may be categorised by the different features it possesses (Perone et al., 2008; Hammer et al., 2009). Cows and horses are both ungulates. They have four legs and a tail, but so does a dog; thus more detail is required to sub-categorise. This can form an progressively specific, branching structure, which the animal can build on through learning (2.2.2). This process is aided by a sensorimotor apparatus that especially attends to functional differences between object categories, rather than more aesthetic differences. This same apparatus would also attend more to perceived differences within a category (i.e. the unexpected), rather than between categories.

This kind of structure would allow for parallel processing at all levels, but there would also be interaction between different groups. This kind of idea has been developed through several neural network models (e.g. Quartz, 1999; Carruthers, 2006; Op de Beeck and Baker, 2010; Shanahan, 2012). The problem comes when there is a combinatorial explosion: too much information is stored in this structure that the system actually becomes slower. For instance, there is a huge search space involved in combining different perceptions, motor sequences, and exploratory behaviours to fit specific shapes, sizes, and object relations (Bellman, 1961; Perlovsky, 1998).

3.3. Combination of 'simple' learning mechanisms

When the environment is too variable, evolution cannot discover in advance suitable fixed responses to all needs in all situations (subsection 2.5). Instead, it provides mechanisms of learning and development that use information about the environment. There should be a selection of simple learning mechanisms, each specialised for particular exploration domains, which allow animals to attend to and learn about stimuli from restricted classes of environment (e.g. Karmiloff-Smith, 1995; subsection 3.2). This enables individuals to discover useful new actions, threats and opportunities. However, these discoveries must start from some initial motivations of some form.

The vast majority of the cognitive scientists are transfixed with arguing for each learning mechanism in isolation and do not consider them in tandem. We propose animals start exploring the world around them using a combination of different mechanisms, which includes (but not restricted to) associative learning (e.g. Rescorla, 1968), trial-and-error learning (e.g. Krueger and Dayan, 2009; Muller, 2010), and probabilistic learning, perhaps using some form of Bayesian networks (e.g. Spirtes et al., 2000; Tenenbaum and Niyogi, 2003).

Initial exploratory behaviours may appear random, where the animal tries lots of different behaviours on lots of different things it knows little about (trial-and-error). However, when it starts to detect the invariances and regularities (through some crude type of probabilistic learning), it starts to narrow down the different possible causal relationships (of different object categories, subsection 3.2). This will be guided by the sensorimotor selectivities described in subsection 3.1.

Quite a large time investment is needed in these relatively simple learning mechanisms. It is important not to discount the impact of simple learning mechanisms in attaining quite sophisticated competences and behaviours (even for humans; Shanks, 2007). However, there is accumulating evidence about the involvement of top-down processes in human and non-human animals, such as causal reasoning and, more recently, probabilistic-driven causal inferences (subsection 4.2).

3.4. Behaviour structured to maximise information gain

Physical actions on the world are very important for the individual to reveal the processes present and objects' invisible affordances (Ravishankar et al., 2008). It is widely accepted human infants' understanding of object properties derives from both their exploratory behaviour and the information-processing systems generating and modifying their behaviour (Gibson, 1988; Gibson and Pick, 2003; Piaget, 1952; Rochat, 2001). In turn, the representations resulting from such activity alter and direct the actions infants perform on objects (Perone et al., 2008).

The combination of strategies used are likely dependent both on the environmental conditions and the individual's own competences. Children learn much quicker, for instance, when they explore objects themselves, rather than watching others (e.g. Fagard and Lockman, 2010; Heyes, 2011; Jacquet et al., 2012).

There has been much less work on the form and function of the information-gathering aspects of exploration in non-human animals (Kacelnik, 1987; Renner, 1990; Inglis, 1983; Inglis et al., 2001; Power, 2000)[7]. What we do know, suggests animals' sensorimotor behaviour acts to increase the quantity and quality of information gained. Many species show active information gathering. Rats alter the speed and pattern of their whisking behaviour to increase information about shape and texture of objects they contact with their vibrissae (Grant et al., 2009). This has been confirmed by modelling the behaviour in a robot (Pearson et al., 2007). The rats' whisking behaviour is 'designed' to increase the probability of detecting important environmental features.

Some of an animal's exploratory behaviours will involve only its body parts – whether limbs, eyes or the whole body (chapter 3). Others will also involve certain objects, where the individual may repeatedly grab, push, pull or twist the same thing. In more complex manipulations, there can be several objects and object parts involved – for instance in stacking or arranging them (for further examples see Appendix C). Whatever level of exploratory complexity, the behaviours would likely be focussed on any changes detected in the environment, especially in an object's affordances (function).

Different exploration domains are often interleaved, such as in alternating between eating and playing with food. This allows knowledge of different domains to develop roughly in parallel (Bushnell and Boudreau, 1993; subsection 5.3). When switching domains, the individual needs to be able to group bits of information together according to the current domain involved. For example, certain materials such as sticks may have one kind of affordance in the tool-using domain, but others when building a nest. For different species, the objects and their affordances will differ according to individuals' ecological niche, but there are probably some common exploration mechanisms across species (Sloman and Chappell, 2005; Chappell and Sloman, 2007).

It is often difficult to distinguish exploratory behaviour from executive action: is the animal lifting an object to transport it, or to learn its weight? Of course, it may fulfil both goals simultaneously (e.g. Elner and Hughes, 1978), but for researchers to determine when (or whether) an animal is simply collecting perceptual information, they need detailed knowledge about the extent of its sensory realm (Demery et al., 2011). We also need reliable behavioural or physiological 'markers' of exploratory behaviour in non-human animals (Section 6).

3.5. Preference for novelty

Neophilia has been shown to be an important aspect of exploration in non-human animals (Greenberg and Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002), and is often associated with the juvenile phase of animals' development (e.g. Heinrich, 1995; Pellegrini et al., 2007). By definition, animals do not have adequate information about novel objects, places and events, so they should prioritise their interaction with them. In particular, animals in dynamic environments might use exploration to experiment with strategies or behaviours in the current environmental context.

Ruff (1986) hypothesised that if the main function of 'examining' behaviour in human infants is to

[7] This does not include studies of the current or future fitness benefits of the behaviour usually referred to as 'play' (Pellegrini et al., 2007; Bekoff and Byers, 1998; Held and Spinka, 2011).

gather information, it should:

1. decrease in frequency with exposure to a particular object;
2. and occur before other behaviours with new objects.

She found both hypotheses were upheld. Additionally, the latency and duration of examination indicated different features of the process, with latency reflecting the time it takes to activate the information-gathering system.

Not all aspects of novelty may be equally salient. Perone et al. (2008) presented infants with an image sequence, depicting a hand acting on a colourful toy that produced a sound, followed by either the action-sound pair or the object's appearance changing. They found infants attended more to changes in action than appearance. From an evolutionary perspective, it is not clear why such salience differences exist, but perhaps appearance changes are less likely to have important implications for the object's function.

4. Stage II: testing hypotheses

We propose in the second stage of exploration, the animal tests its internal hypotheses. Its exploratory behaviours are targeted more selectively, according to the specific object and environmental problem presented (subsection 4.3). The animal uses progressively more complex learning mechanisms like causal reasoning (subsection 4.2), so exploratory behaviours become less repetitive (unlike in subsection 3.3). Consequently it can cope with more complex problems, such as an apparatus with multiple object relations (e.g. Miyata et al., 2011). This is aided by a pre-existing biological framework of physical rules, particularly object solidity, continuity and connectedness (subsection 4.1). When its theories are violated, greater exploration ensues (subsection 4.4).

4.1. Sensitivity to physical rules

There are certain aspects of the physical world that can be regarded as constants (subsection 2.1). This includes gravity, the properties of contact, solidity, and biological movement or agency. Exploring animals probably harness these features as defaults ('basic physical rules') from birth or hatching. This enables them to have some basic understanding of how the world should work and how objects should interact.

Although somewhat contentious (e.g. Karmiloff-Smith, 1995), the extensive developmental work of Spelke and colleagues (summarised in Spelke, 2000) demonstrates human infants probably have innate systems representing objects, number and space. Developing alternative developmental methods should clarify these ideas further. This has begun with some non-human animal work on juveniles (e.g. Funk, 2002; Zucca et al., 2007; Bird and Emery, 2010). This has been extended to adult animals to show at least some species have such pre-dispositions (e.g. Hauser et al., 1999; Kundey et al., 2010; Cacchione and Call, 2010; Jaakkola et al., 2010; O'Connell and Dunbar, 2005, on solidity). These are fine-tuned and built upon with experience (Section 5).

There is likely, however, a distinction between individuals' implicit (subconscious) and explicit (conscious) understanding of a situation. There is a difference between noting a causal relation is wrong (e.g. a floating block) and predicting how it should be (see also subsection 4.4). Previously, this dichotomy has been differentiated in developmental psychology by presenting infants with impossible events, then measuring looking-times and where they search/explore in the test apparatus.

4.2. Combination of 'complex' learning mechanisms

As animals progress they likely use a selection of successively more complex learning mechanisms (e.g. 'causal reasoning'), coupled with simpler mechanisms (subsection 3.3). An animal may start out gathering information about a particular domain using probabilistic learning. When that no longer yields information, yet there is still a known gap in their knowledge (subsection 5.2), the information-processing system becomes more generative in some way. This allows it to notice deep invariances between examples, which previously were thought to share an object category (see also subsection 3.2 and subsection 4.4). The question is what process drives this internal transition.

Unlike trial-and-error and probabilistic learning, some prediction is possible without haptic exploration. Causal understanding of different struc-

tures' functions is made possible by reasoning through different possibilities (e.g. Blaisdell et al., 2006; Darredeau et al., 2009). An individual may utilise several concepts and mechanisms of causal reasoning, depending on the causal problem they face (e.g. canopy route planning; Tecwyn et al., 2012).

A formal, specific model is yet to be determined. A hierarchical structure may be the answer (subsection 2.2.2). The number of learning strategies used in a particular domain may determine the structure's number of levels. To activate a new level of a set of concepts, lower levels may need to be acquired first, through particular learning mechanisms. For example, relevant objects or relationships could be identified by probabilistic mechanisms that detect correlations (e.g. Chater et al., 2006). Once those correlations have been found, incorporating them as neural network nodes (e.g. Quartz, 1999; Marcus, 2003) allows new pattern learning. This combination of objects and patterns can feed an inference system (e.g. Ackerman and Others, 2004; subsection 5.1) for building new concepts. To varying extents, these mechanisms can be revealed through observing spontaneous exploratory behaviour (Section 6).

4.3. Behaviour more targeted and selective

Assuming the function of exploratory behaviour is to gather information, we would expect its form (and underlying mechanisms) to change with context (see also subsection 3.4). Each type of exploratory behaviour generates perceptual changes best suited to the sensory modality used (subsection 3.1), maximising opportunities to detect relevant features (subsection 2.4).

The type of manipulations human infants employ alter with how various toys' affordances change. When an object's texture changes, the looking and fingering of it increases (Ruff, 1984). In contrast, shape changes lead to increased rotation and transfer of the object between hands. Similarly, while looking at the object, infants are more likely to transfer it between hands, or finger its surface, but while mouthing it, they are more likely to rotate it (Ruff et al., 1992).

Renner and colleagues (Renner and Rosenzweig, 1986; Renner and Seltzer, 1994) showed rats employed different types of exploratory behaviours when there was potential to gain more information. The relative frequencies, sequences and complexities of different exploratory behaviours varied according to previous experience and particular object characteristics. Heyser and Chemero (2012) showed mouse (*Mus musculus domesticus*) exploration levels and actions displayed depended on functional cues of a novel object, rather than purely visible, aesthetic cues.

4.4. Active 'testing' when expectations are violated

If an organism's current empirical observations do not fit with previously collected information, it should re-initiate exploration to resolve this discrepancy. There is increasing evidence human children use a conditional intervention principle to resolve discrepancies and learn about causes (Gopnik, 1996; Gopnik and Schulz, 2004; Tenenbaum et al., 2006). Their exploration appears to be systematic and sensitive to ambiguous information (see also subsection 5.2). Schulz et al. (2008) presented blocks of a certain category magnetically sticking to a board. When children found properties of new blocks varied within the category, they explored more.

There are several different, inter-linked processes here. The individual needs to detect some aspect of the world is surprising; then commence exploration, focussing on resolving this. The latter may involve re-organisation, or other changes in representations (e.g. see subsection 5.3). There is again much less literature on non-human animals. Some studies have manipulated certain environmental stimuli and measured exploratory behavioural sequences (Bekoff, 1975; Renner, 1990; Kuba et al., 2006). At least in rats and octopi (*Octopus vulgaris*), these revealed behaviour ostensibly similar to human children. As far as we know, there have been no studies into whether non-human animals spontaneously perform their own 'tests' like human children (Povinelli and Dunphy-Lelii, 2001; Buchsbaum et al., 2012). We predict non-human animals, like children, would become less repetitive in their exploratory actions as they develop – they would display greater diversity of exploratory behaviours, rather than repeating a few actions on the same part of the environment. This would allow them to learn what kinds of actions would be most effective in different situations.

The ability to deal with surprises and test unknown elements is limited by the potential of the learning mechanisms utilised and the form of the information representation (e.g. difficult with the simple mechanisms described in subsection 3.3). Some models, such as artificial neural networks, relying on a series of weighted associations, fall short in explaining this behaviour (e.g. Quartz, 1999). These models do not always make clear what associations the simulated individual is acquiring. However, logical, symbolic models allow researchers to produce demonstrations of the simulated individual's exploration pattern (e.g. Arriola-Rios et al., 2012).

5. Stage III: extending and refining hypotheses

In the final stage, we propose animals extend and refine their hypotheses. They analyse their theories and re-use information, combining them in related, but new, environmental situations (subsection 5.3). Individuals can now use causal inference to abstractly fill information gaps (subsection 5.1), extending hypotheses throughout life. This is especially important in a dynamic environment, where the animal should seek to test its current models, particularly when its expectations are violated (like in the previous stage; subsection 4.4). These abilities imply meta-cognitive mechanisms and an endogenous motivation to fill in the identified gaps of information (subsection 5.2).

5.1. Causal inference by abstracting information

Animals explore more efficiently if they are guided by previous knowledge of hidden object features to causally infer potential, new information. Information is usually acquired in a format of restricted use (subsection 3.3). If animals find generalisations by abstracting across different types of information, the information has greater use, particularly for solving causal problems. After subsequent experiences, to use the stored structures for specific functions, animals need to re-organise information into a new generative form. This form has wider scope, so it is both more economical and powerful. It is a deductive system for deriving novel conclusions (i.e. 'representational redescription'; Karmiloff-Smith, 1995).

A prominent example is the transition in human children from using empirically learnt words to generative syntax. An infinite number of sentences can now be generated and understood. Other animals demonstrate a simpler form of this cognitive flexibility to access food resources. They apply elements of existing knowledge about particular behaviours in one environmental context, to an entirely new context (e.g. keas and crows in Auersperg et al., 2011).

There is evidence that a number of taxa (e.g. apes, rats and dogs) can make causal inferences using multiple information sources (see also subsection 5.1). Some can harness information from the object itself (e.g. weight; Blaisdell et al., 2006; Call, 2004; Brauer et al., 2006; Hanus and Call, 2008), social cues (e.g. Povinelli et al., 1990), or by exclusion (Aust et al., 2008; Hill et al., 2011; Call, 2006). However, these experiments relied on animals observing the state of the world, or watching others perform actions on objects.

The mechanisms underlying abstraction processes are still debatable. Sidman (e.g. 2000) proposed several concepts (e.g. symmetry or transitivity) are acquired purely as a consequence of reinforcement contingencies. This has been supported by experiments on captive pigeons (*Columba livia*) using successive matching (Urcuioli, 2008). However, these experiments involved a small number of familiar, simple stimuli, presented under tightly constrained learning conditions. Whether they are ecologically valid, or can be extended to the field, is unclear. The natural world can offer a rich array of complex details and contributing factors (discussed in chapter 5), where consequences of actions need to be reasoned out, rather than retrieved from memory. What the reinforcement might be in such cases is not apparent, nor can the mechanisms proposed by Sidman (2000) readily explain a deductive system similar to that described above.

A flexible, abstractive system can re-organise and re-represent information from one domain to generalise others. This later allows for the original domain to become an object of exploratory attention. Individuals can then question issues such as what may occur within that domain (subsection 5.3). Such abstractive and causal inference systems aids information-gathering about invisible affordances or structures. Particularly important information may be several steps along from the initial

exploratory behaviour, or only become apparent once acted upon (e.g. object permanence concept with hidden object; see subsection 4.1).

5.2. *Meta-cognitive ability to recognise gaps in knowledge*

When there is a lack of information in the environment, animals would benefit from being able to track their own level of uncertainty (e.g. Inglis et al., 2001). For instance, when making a decision, an animal should be aware if it lacks sufficient information. There are many forms of meta-cognition (i.e. self-awareness; e.g. Karmiloff-Smith, 1995; Povinelli and Preuss, 1995), but in this chapter we refer specifically to self-directed meta-cognition. It has been difficult to establish evidence of this kind of meta-cognition in animals (for a review see Smith, 2009) and there are few biologically plausible, working models.

There may be some self-organising knowledge stores, reacting automatically to changes and new opportunities. In other cases, the information-processing system may possess a separate sub-system. This could monitor other sub-systems' behaviour and detect opportunities to initiate major re-organisation (e.g. Sussman, 1973). For example, when objects behave contrary to their appearance (as in subsection 4.4), the animal is stimulated to perform more exploration.

In Stage III, animals are capable of representing different scenarios in their past, present and future. After the results of an exploratory behaviour are observed, this capability together with meta-cognition/uncertainty, enables thoughts about what could have been ('counterfactual thinking'). Such abilities have again been described in human children (Beck et al., 2008; Byrne, 2002), but much less in other animals (e.g. Seed et al., 2012). Children explore more and target their behaviours (subsection 4.3) when faced with ambiguous information and their own uncertainty (summarised in Schulz, 2012).

Self-criticism mechanisms can further aid learning by improving problem-solving skills (Sussman, 1973; Sloman, 2008b). These mechanisms may initially be genetically-encoded, but their effects vary according to individuals' experience. Different forms of learning develop throughout life, influenced by the genome *and* the environment. For example, humans learning about advanced mathematical concepts need to first develop various forms of representation, allowing understanding of progressively abstract structures and processes. These types of learning differ from earlier forms not just in their content, but in their structure.

5.3. *Extending knowledge by combining domains*

Combining old exploration domains can create new ones. One common simplification by animals is the discovery that two domains, involving different perceptual contents and affordances, can share structures and be unified into a useful, new abstraction. This can be applied to existing exploration domains and form new domains. For instance, in combining information about soil with information about water, to form knowledge about mud. Abstractions about physical rules can be applied to several exploration domains (e.g. cohesiveness; subsection 4.1).

Such combinations are made possible by several domains representing spatial structures and processes – behaviours originally performed at different locations or times, can later be performed together. This can lead to new forms of interaction (e.g. Taylor et al., 2009; Miyata et al., 2011). In some cases, what was previously learnt in separate domains, enable an animal to predict and reason about novel concepts. In other cases, more empirical learning is required, followed by meta-cognition (subsection 5.2) and new forms of theory re-construction (e.g. about mud properties).

It is not clear how the many environmental properties represented in adults as numerical measures (e.g. position, velocity, volume; Rheingold, 1985) can be represented in a young learner. Karmiloff-Smith (1995) emphasised how, in humans, sometimes competences gained at one developmental stage, can be later revised or transformed at another developmental stage.

It is difficult to determine whether this is due to internal re-organisation, or whether a separate meta-cognitive system is required. Cognitive robotics can reveal some alternative models, along with their implications, costs, and demonstrations of what is possible (e.g. Lopes and Oudeyer, 2010). We propose animals extend hypotheses throughout life, as suggested by the high level of neophilia in cognitively flexible and long-lived organisms

(e.g. parrots; Luescher, 2006).

6. Testing exploratory learning

By observing exploratory behaviour, we can gain an insight into how different animals gather information and learn about the world around them. It is challenging to explicitly discriminate between the different underlying learning mechanisms employed at any given moment. Instead cognitive scientists should use exploration to *frame* what an animal is doing and what types of information they may be collecting. Then we can begin to discuss how the exploratory behaviour observed under different conditions might fit into different learning mechanisms.

With this approach in mind, we have presented a general three-stage theory for how different animals can gather different kinds of information throughout their lives. The details likely vary between different species, individuals, exploratory domains and environmental situations. This theory was purposefully designed as a general framework, so it can be applied to a wide range of contexts. The theory is an example of how apparently different forms of thinking from different research fields (discussed in chapter 1) can be integrated to provide a fuller account of the research problem. This provides diverse opportunities for interdisciplinary collaboration and further systematic investigation.

For instance, in Arriola-Rios and Demery (2012), we explored how a parrot may internally represent different forms of objects' compliance, using techniques from artificial intelligence. A working preliminary model of object compliance, using specific physical rules and probabilistic learning, was compared with behavioural results collected from live animals (from experiments discussed in chapter 6)[8]. We showed how a selection of key elements from the environment (a form of categorisation) could be used as a basis for efficiently representing objects and their related processes (e.g. a sponge being squeezed).

[8]This was just a correlational comparison. In this study, we could not confirm if the observed parrot exploration was due to similar underlying mechanisms as those presented in the artificial model.

In the future, we hope to apply this same artificial model to a range of materials and problem-solving tasks (as in e.g. Arriola-Rios and Savage, 2007). A selection of 'built-in properties' that a 'virtual parrot' may have are described in Appendix E. This has been shown to work in a very basic simulated environment using StarLogo TNG version 1.5 (Colella et al., 2001). To check the ecological validity of these artificial models, they should be verified against a wider range of biological examples, under different experimental conditions.

The theory described in this chapter provides a framework for forming testable hypotheses. We chose to study two exemplar exploratory species; kakariki (*Cyanoramphus novaezelandiae*) and humans. There is much less literature on exploration in non-human animals, so in the kakariki tests we focused on the earlier stages of exploration (Section 3 and parts of Section 4). In the human tests, we focused on the later stages of exploration (Section 4 and Section 5), which have been neglected in the human exploration literature. Thus, in chapter 6 we hypothesise kakariki will explore more with:

- the corners and curves of objects over flat surfaces (due to points explained in subsection 3.1);
- increasing object complexity (due to points explained in subsection 3.4);
- novel over familiar objects (subsection 3.5);
- functional, invisible changes in an object over less functional or aesthetic changes, especially if the change occurs within-category (rather than between-category; subsection 3.2);
- unexpected changes in an object (i.e. if the haptic cues contradict the visual cues; subsection 4.4);
- extreme object categories first, but with time will explore the intermediate categories more (subsection 3.2 and subsection 3.4).

Further, in chapter 7 we hypothesise that human children will explore more:

- functional/action changes in an object than aesthetic changes (like the kakariki; due to point explained in subsection 3.2);

- when a change in a physical rule has occurred (subsection 4.1), and the initial exploratory behaviour will be directed at the change's source (subsection 4.2), rather than the (usually now functionless) object area previously habituated to (subsection 3.3);

- when there is missing or ambiguous information (and causal inferences are needed; subsection 5.1 and subsection 5.2);

- when older (in terms of behavioural diversity; subsection 4.3) and there will be a developmental shift across different exploratory domains (subsection 5.3).

Ackerman, B. P., Others, A., Oct. 2004. Building a story representation: the effects of early concept prominence on later causal inferences by children. Developmental Psychology 27 (3), 370–80. 4.2

Albert, D. J., Mah, C. J., 1972. An examination of conditioned reinforcement using a one-trial learning procedure. Learning and Motivation 3, 369–388. 2.1

Alkon, D. L., Lederhendler, I., Shoukimas, J., Feb. 1982. Primary changes of membrane currents during retention of associative learning. Science 215 (4533), 693–695. 2.2

Arriola-Rios, V. E., Demery, Z. P., 2012. Salient features and snapshots in time: an interdisciplinary perspective on object representation. In: Proceedings of the Symposium on Natural/Unconventional Computing and its Philosophical Significance at the AISB/IACAP World Congress 2012. pp. 1–6. 6

Arriola-Rios, V. E., Demery, Z. P., Wyatt, J., Sloman, A., Chappell, J., Jul. 2012. Salient features and snapshots in time: an interdisciplinary perspective on object representation. In: Crnkovic, G. D., Giovagnoli, R. (Eds.), Studies in Applied Philosophy, Epistemology and Rational Ethics: Computing Nature. Springer, Berlin, pp. 1–14. (document), 4.4

Arriola-Rios, V. E., Savage, J., 2007. Knowledge Acquisition and Automatic Generation of Rules for the Inference Machine CLIPS. In: Gelbukh, A. F., Kuri Morales, A. F. (Eds.), MICAI 2007: Advances in Artificial Intelligence, 6th Mexican International Conference on Artificial Intelligence. Springer, Aguascalientes, Mexico, pp. 725–735. 2.2.2, 6

Auersperg, A., von Bayern, A. M. P., Gajdon, G. K., Huber, L., Kacelnik, A., 2011. Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. PloS One 6 (6), e20231. 2.5, 5.1

Aust, U. U., Range, F., Steurer, M., Huber, L., Oct. 2008. Inferential reasoning by exclusion in pigeons, dogs, and humans. Animal Cognition 11 (4), 587–597. 5.1

Avargues-Weber, A., Portelli, G., Benard, J., Dyer, A. G., Giurfa, M., Feb. 2010. Configural processing enables discrimination and categorization of face-like stimuli in honeybees. Journal of Experimental Biology 213 (4), 593–601. 3.2

Beck, S. R., Robinson, E. J., Freeth, M., Apr. 2008. Can children resist making interpretations when uncertain? Journal of Experimental Child Psychology 99 (4), 252–270. 5.2

Bekoff, M., 1975. Animal play and behavioral diversity. American Naturalist 109 (969), 601–603. 4.4

Bekoff, M., Byers, J. A., 1998. Animal Play: Evolutionary, Comparative, and Ecological Perspectives. Evolutionary, Comparative and Ecological Perspectives. Cambridge University Press, Cambridge, UK. 7

Bellman, R. E., 1961. Adaptive control processes: a guided tour. Princeton University Press, Princeton, NJ. 3.2

Ben-Jacob, E., Oct. 2009. Learning from bacteria about natural information processing. Annals of the New York Academy of Sciences 1178, 78–90. 5

Berlyne, D. E., 1960. Conflict, arousal, and curiosity. McGraw-Hill Book Company, New York, NY, US. 1

Bird, C. D., Emery, N. J., Jan. 2010. Rooks perceive support relations similar to six-month-old babies. Proceedings of the Royal Society of London B: Biological Sciences 277 (1678), 147–151. 4.1

Blaisdell, A. P., Sawa, K., Leising, K. J., Waldmann, M. R., Jan. 2006. Causal reasoning in rats. Science 311 (5763), 1020–1022. 4.2, 5.1

Brauer, J., Kaminski, J., Riedel, J., Call, J., Tomasello, M., Feb. 2006. Making inferences about the location of hidden food: social dog, causal ape. Journal of Comparative Psychology 120 (1), 38–47. 5.1

Buchsbaum, D. D., Bridgers, S. S., Weisberg, D. D. S., Gopnik, A., Sep. 2012. The power of possibility: causal learning, counterfactual reasoning, and pretend play. Philosophical Transactions of the Royal Society B: Biological Sciences 367 (1599), 2202–2212. 4.4

Bushnell, E. W., Boudreau, J. P., Aug. 1993. Motor development and the mind: the potential role of motor abilities as a determinant of aspects of perceptual development. Child Development 64 (4), 1005–1021. 3.4

Byrne, R. M. J., Oct. 2002. Mental models and counterfactual thoughts about what might have been. Trends in Cognitive Sciences 6 (10), 426–431. 5.2

Cacchione, T., Call, J., 2010. Intuitions about gravity and solidity in great apes: the tubes task. Developmental Science 13 (2), 320–330. 4.1

Call, J., Jun. 2004. Inferences about the location of food in the great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo pygmaeus*). Journal of Comparative Psychology 118 (2), 232–241. 5.1

Call, J., Oct. 2006. Inferences by exclusion in the great apes: the effect of age and species. Animal Cognition 9 (4), 393–403. 5.1

Calvo, P., Gomila, T., Gomila, A., 2008. Handbook of Cognitive Science: An Embodied Approach. Vol. New York. Elsevier, London. 1

Carruthers, P., 2006. The Architecture of the Mind: Massive Modularity and the Flexibility of Thought: massive modularity and the flexibility of thought. Clarendon Press, London. 3.2

Chappell, J., Demery, Z. P., Arriola-Rios, V. E., Sloman, A., Feb. 2012. How to build an information gathering and processing system: lessons from naturally and artificially intelligent systems. Behavioural Processes 89 (2), 179–186. (document), 2

Chappell, J., Sloman, A., 2007. Natural and Artificial Meta-Configured Altricial Information-Processing Systems. International Journal of Unconventional Computing 2 (3), 211–239. 1, 2.5, 3.4

Chater, N., Tenenbaum, J. B., Yuille, A., Jul. 2006. Probabilistic models of cognition: conceptual foundations. Trends in Cognitive Sciences 10 (7), 287–291. 4.2

Colella, V., Klopfer, E., Resnick, M., Jun. 2001. Adventures in Modeling: Exploring Complex, Dynamic Systems with StarLogo. Teachers College Press, London. 6

Cook, C., Goodman, N. D., Schulz, L. E., Sep. 2011. Where

science starts: Spontaneous experiments in preschoolers exploratory play. Cognition 120 (3), 341–349. 2.6

Darredeau, C., Baetu, I., Baker, A. G., Murphy, R. A., Jan. 2009. Competition between multiple causes of a single outcome in causal reasoning. Journal of Experimental Psychology: Animal Behavior Processes 35 (1), 1–14. 4.2

Demery, Z. P., Arriola-Rios, V. E., Sloman, A., Wyatt, J., Chappell, J., 2010. Construct to understand: learning through exploration. In: Proceedings of the International Symposium on AI-Inspired Biology. pp. 59–61. (document), 1

Demery, Z. P., Chappell, J., Martin, G. R., Dec. 2011. Vision, touch and object manipulation in Senegal parrots *Poicephalus senegalus*. Proceedings of the Royal Society of London B: Biological Sciences 278 (1725), 3687–3693. 1, 3.4

Elner, R., Hughes, R. N., 1978. Energy maximization in the diet of the shore crab, Carcinus maenas. Journal of Animal Ecology 47 (1), 103–116. 3.4

Fabre, J. H., de Mattos, A. T., Miall, B., 1918. The wonders of instinct. The Century Co., Minnesota. 2.1

Fagard, J., Lockman, J., Jan. 2010. Change in imitation for object manipulation between 10 and 12 months of age. Developmental Psychobiology 52 (1), 90–99. 3.4

Flanagan, J. R., Wing, A. M., Feb. 1997. The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. Journal of Neuroscience 17 (4), 1519–1528. 3.1

Floreano, D., Mattiussi, C., 2008. Bio-Inspired Artificial Intelligence: Theories, Methods, and Technologies. MIT Press, Cambridge, MA. 3.1

Funk, M. S., Sep. 2002. Problem solving skills in young yellow-crowned parakeets (*Cyanoramphus auriceps*). Animal Cognition 5 (3), 167–176. 4.1

Gibson, E. J., Jan. 1988. Exploratory behavior in the development of perceiving, acting, and the acquiring of knowledge. Annual Reviews of Psychology 39 (1), 1–42. 1, 2.6, 3.1, 3.4

Gibson, E. J., Pick, A., 2003. An Ecological Approach to Perceptual Learning and Development. Oxford University Press, New York. 3.4

Gibson, J. J., Nov. 1962. Observations on active touch. Psychological Review 69, 477–491. 1

Gibson, J. J., 1977. The theory of affordances. In: Shaw, R., Bransford, J. (Eds.), Perceiving, acting, and knowing: Toward an ecological psychology. Erlbaum, Hillsdale, NJ, pp. 67–82. 3.1

Giret, N., Peron, F., Nagle, L., Kreutzer, M., Bovet, D., Nov. 2009. Spontaneous categorization of vocal imitations in African grey parrots (*Psittacus erithacus*). Behavioural Processes 82 (3), 244–248. 3.2

Glickman, S. E., Sroges, R. W., 1966. Curiosity in zoo animals. Behaviour 26 (1), 151–188. 1

Gopnik, A., Dec. 1996. The Scientist as Child. Philosophy of Science 63 (4), 485–514. 4.4

Gopnik, A., Schulz, L. E., Aug. 2004. Mechanisms of theory formation in young children. Trends in Cognitive Sciences 8 (8), 371–377. 4.4

Grant, R. A., Mitchinson, B., Fox, C. W., Prescott, T. J., Feb. 2009. Active touch sensing in the rat: anticipatory and regulatory control of whisker movements during surface exploration. Journal of Neurophysiology 101 (2), 862–874. 3.4

Greenberg, R., Mettke-Hofmann, C., 2001. Ecological aspects of neophobia and neophilia in birds. In: Nolan, V., Thompson, C. F. (Eds.), Current Ornithology. Springer, Boston, MA, pp. 119–178. 2, 3.5

Hammer, R., Diesendruck, G., Weinshall, D., Hochstein, S., Jun. 2009. The development of category learning strategies: What makes the difference? Cognition 112 (1), 105–119. 3.2

Hanus, D., Call, J., May 2008. Chimpanzees infer the location of a reward on the basis of the effect of its weight. Current Biology 18 (9), R370–R372. 5.1

Hauser, M. D., Kralik, J., Botto-Mahan, C., 1999. Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus oedipus oedipus*. Animal Behaviour 57, 565–582. 4.1

Hawes, N., Hanheide, M., Sjoo, K., Aydemir, A., Jensfelt, P., Gobelbecker, M., Brenner, M., Zender, H., Lison, P., Kruijff-Korbayova, I., Kruijff, G. J. M., Zillich, M., May 2010. Dora the Explorer: a motivated robot. In: Proceedings of the 9th International Conference on Autonomous Agents and Multiagent Systems. International Foundation for Autonomous Agents and Multiagent Systems, pp. 1617–1618. 1

Heinrich, B., 1995. Neophilia and exploration in juvenile common ravens, *Corvus corax*. Animal Behaviour 50 (3), 695–704. 3.5

Held, S., Spinka, M., 2011. Animal play and animal welfare. Animal Behaviour 81, 891–899. 7

Heyes, C., Sep. 2011. What's social about social learning? Journal of Comparative Psychology 126 (2), 193–202. 3.4

Heyser, C. J., Chemero, A., Mar. 2012. Novel object exploration in mice: not all objects are created equal. Behavioural Processes 89 (3), 232–238. 4.3

Hill, A., Collier-Baker, E., Suddendorf, T., Feb. 2011. Inferential reasoning by exclusion in great apes, lesser apes, and spider monkeys. Journal of Comparative Psychology 125 (1), 91–103. 5.1

Horner, V., Whiten, A., Jun. 2005. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). Animal Cognition 8 (3), 164–181. 2.4

Houston, A. I., Krebs, J. R., Erichsen, J. T., Jan. 1980. Optimal prey choice and discrimination time in the great tit (*Parus major L.*). Behavioral Ecology and Sociobiology 6 (3), 169–175. 2.5

Huber, L., Gajdon, G. K., Sep. 2006. Technical intelligence in animals: the kea model. Animal Cognition 9 (4), 295–305. 2.5

Inglis, I. R., Nov. 1983. Towards a cognitive theory of exploratory behaviour . In: Archer, J., Birke, L. I. A. (Eds.), Exploration in Animals and Humans: comparative psychology of animals and humans. Van Nostrand Reinhold, Workingham, pp. 72–117. 1, 3.4

Inglis, I. R., Langton, S., 2006. How an animal's behavioural repertoire changes in response to a changing environment: a stochastic model. Behaviour 143, 1563–1596. 1

Inglis, I. R., Langton, S., Forkman, B., Lazarus, J., Sep. 2001. An information primacy model of exploratory and foraging behaviour. Animal Behaviour 62 (3), 543–557. 3.4, 5.2

Jaakkola, K., Guarino, E., Rodriguez, M., Erb, L., Trone, M., Jan. 2010. What do dolphins (*Tursiops truncatus*) understand about hidden objects? Animal Cognition 13 (1), 103–120. 4.1

Jacquet, P. O., Chambon, V., Borghi, A. M., Tessari, A., 2012. Object Affordances Tune Observers' Prior Expectations about Tool-Use Behaviors. PloS One 7 (6), e39629. 3.4

Kacelnik, A., Jun. 1987. Information primacy or preference for familiar foraging techniques? A critique of Inglis & Ferguson. Animal Behaviour 35 (3), 925–926. 3.4

Kacelnik, A., Krebs, J. R., 1985. Learning to exploit patchily distributed food. In: Sibly, R. M., Smith, R. H. (Eds.), Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. Blackwell Scientific Publications, Oxford, pp. 189–205. 2.5

Kacelnik, A., Todd, I. A., Feb. 1992. Psychological mechanisms and the Marginal Value Theorem: effect of variability in travel time on patch exploitation. Animal Behaviour 43 (2), 313–322. 2.5

Karmiloff-Smith, A., 1995. Beyond Modularity: A Developmental Perspective on Cognitive Science, 4th Edition. MIT Press, London. 2.2.2, 3.2, 3.3, 4.1, 5.1, 5.2, 5.3

Kelman, E. J., Osorio, D., Baddeley, R. J., May 2008. A review of cuttlefish camouflage and object recognition and evidence for depth perception. Journal of Experimental Biology 211 (11), 1757–1763. 3.2

Krebs, J. R., Kacelnik, A., Taylor, P., Sep. 1978. Test of optimal sampling by foraging great tits. Nature 275 (5675), 27–31. 3.2

Krueger, K. A., Dayan, P., Mar. 2009. Flexible shaping: how learning in small steps helps. Cognition 110 (3), 380–394. 3.3

Kuba, M. J., Byrne, R. M. J., Meisel, D. V., Mather, J. A., Jul. 2006. When do octopuses play? Effects of repeated testing, object type, age, and food deprivation on object play in *Octopus vulgaris*. Journal of Comparative Psychology 120 (3), 184–190. 4.4

Kundey, S. M. A., De Los Reyes, A., Taglang, C., Baruch, A., German, R., May 2010. Domesticated dogs' (*Canis familiaris*) use of the solidity principle. Animal Cognition 13 (3), 497–505. 4.1

Loewenstein, G., 1994. The psychology of curiosity: A review and reinterpretation. Psychological Bulletin 116 (1), 75–98. 1

Loomis, J. M., Beall, A. C., Jan. 1998. Visually controlled locomotion: its dependence on optic flow, three-dimensional space perception, and cognition. Ecological Psychology 10 (3), 271–285. 3.1

Lopes, M., Oudeyer, P.-Y., 2010. Guest Editorial: Active learning and intrinsically motivated exploration in robots: advances and challenges. In: IEEE Transactions on Autonomous Mental Development. pp. 65–69. 5.3

Luescher, A. U., 2006. Manual Of Parrot Behavior. Blackwell, San Francisco. 5.3

Magnani, L., 2009. Abduction, affordances, and cognitive niches. In: Abductive Cognition. Springer, Berlin, pp. 317–359. 1

Marcus, G. F., 2003. The Algebraic Mind: Integrating Connectionism and Cognitive Science. MIT Press, London. 4.2

Markram, H., Feb. 2006. The blue brain project. Nature Reviews Neuroscience 7 (2), 153–160. 1

McCrone, J., 2006. Smarter than the average bug. New Scientist 190 (2553), 37–39. 1

Merleau-Ponty, M., 2002. Phenomenology of Perception. Routledge, London. 3.1

Mesulam, M., Jun. 1998. From sensation to cognition. Brain 121 (6), 1013–1052. 1

Mettke-Hofmann, C., Winkler, H., Leisler, B., 2002. The significance of ecological factors for exploration and neophobia in parrots. Ethology 108 (3), 249–272. 2, 3.5

Miller, N. E., Dollard, J., 1941. Social Learning and Imitation. International Library of Sociology. Yale University Press, New Haven, CT. 1

Miyata, H., Gajdon, G. K., Huber, L., Fujita, K., Jan. 2011. How do keas (*Nestor notabilis*) solve artificial-fruit problems with multiple locks? Animal Cognition 14 (1), 45–58. 4, 5.3

Muller, C. A., Mar. 2010. Do anvil-using banded mongooses understand means-end relationships? A field experiment. Animal Cognition 13 (2), 325–330. 3.3

O'Connell, S., Dunbar, R. I. M., Jan. 2005. The perception of causality in chimpanzees (*Pan* spp.). Animal Cognition 8 (1), 60–66. 4.1

Op de Beeck, H. P., Baker, C. L., Jan. 2010. The neural basis of visual object learning. Trends in Cognitive Sciences 14 (1), 22–30. 3.2

Pearson, M. J., Pipe, A. G., Melhuish, C., Mitchinson, B., Prescott, T. J., Sep. 2007. Whiskerbot: a robotic active touch system modeled on the rat whisker sensory system. Adaptive Behavior 15 (3), 223–240. 3.4

Pellegrini, A. D., Dupuis, D., Smith, P. K., Jun. 2007. Play in evolution and development. Developmental Review 27 (2), 261–276. 7, 3.5

Penn, D. C., Holyoak, K. J., Povinelli, D. J., Apr. 2008. Darwin's mistake: explaining the discontinuity between human and nonhuman minds. Behavioral and Brain Sciences 31 (2), 109–178. 1

Perlovsky, L. I., 1998. Conundrum of combinatorial complexity. IEEE Transactions on Pattern Analysis and Machine Intelligence 20 (6), 666–670. 3.2

Perone, S. S., Madole, K. L., Ross-Sheehy, S., Carey, M., Oakes, L. M., Aug. 2008. The relation between infants' activity with objects and attention to object appearance. Developmental Psychology 44 (5), 1242–1248. 3.2, 3.4, 3.5

Piaget, J., 1952. The Origins of Intelligence in Children. International Universities Press, Michigan. 3.4

Povinelli, D. J., Dunphy-Lelii, S., Jun. 2001. Do chimpanzees seek explanations? Preliminary comparative investigations. Canadian Journal of Experimental Psychology 55 (2), 185–193. 4.4

Povinelli, D. J., Nelson, K., Boysen, S. T., Sep. 1990. Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology 104 (3), 203–210. 5.1

Povinelli, D. J., Preuss, T. M., Aug. 1995. Theory of mind: evolutionary history of a cognitive specialization. Trends in Neurosciences 18 (9), 418–424. 5.2

Power, T. G., 2000. Play and Exploration in Children and Animals, 1st Edition. Psychology Press, London. 3.4

Qin, J., Wheeler, A. R., Feb. 2007. Maze exploration and learning in *C. elegans*. Lab on a Chip 7 (2), 186–192. 5

Quartz, S. R., Feb. 1999. The constructivist brain. Trends in Cognitive Sciences 3 (2), 48–57. 3.2, 4.2, 4.4

Ravishankar, S., Jain, A., Mittal, A., 2008. Multi-stage contour based detection of deformable objects. In: Computer Vision ECCV 2008. pp. 483–496. 3.4

Renner, M. J., 1990. Neglected aspects of exploratory and investigatory behavior. Psychobiology 18 (1), 16–22. 1, 3.4, 4.4

Renner, M. J., Rosenzweig, M. R., 1986. Object interactions in juvenile rats (*Rattus norvegicus*): effects of different experiential histories. Journal of Comparative Psychology 100 (3), 229–236. 4.3

Renner, M. J., Seltzer, C. P., 1994. Sequential structure in behavioral components of object investigation by Long-Evans rats (*Rattus norvegicus*). Journal of Comparative Psychology 108 (4), 335. 4.3

Rescorla, R. A., Aug. 1968. Probability of shock in the presence and absence of CS in fear conditioning. Journal of Comparative and Physiological Psychology 66 (1), 1–5. 3.3

Rheingold, H. L., 1985. Development as the acquisition of familiarity. Annual Review of Psychology 36, 1–18. 5.3

Rochat, P., 2001. The Infant's World. Harvard University Press, Cambridge, MA. 1, 3.4

Rosenheim, J. A., 1987. Nesting behavior and bionomics of a solitary ground-nesting wasp, *Ammophila dysmica* (Hymenoptera: Sphecidae): influence of parasite pressure. In: Annals of the Entomological Society of America. Entomological Society of America, pp. 739–749. 2.1

Ruff, H. A., 1984. Infants' manipulative exploration of objects:

Effects of age and object characteristics. Developmental Psychology 20 (1), 9–20. 4.3

Ruff, H. A., Feb. 1986. Components of attention during infants' manipulative exploration. Child Development 57 (1), 105–114. 3.5

Ruff, H. A., Saltarelli, L. M., Capozzoli, M., Dubiner, K., 1992. The differentiation of activity in infants' exploration of objects. Developmental Psychology 28 (5), 851–861. 4.3

Schulz, L. E., Jul. 2012. The origins of inquiry: inductive inference and exploration in early childhood. Trends in Cognitive Sciences 16 (7), 382–389. 5.2

Schulz, L. E., Bonawitz, E. B., Jun. 2007. Serious fun: preschoolers engage in more exploratory play when evidence is confounded. Developmental Psychology 43 (4), 1045–1050. 1

Schulz, L. E., Sommerville, J., 2006. God does not play dice: Causal determinism and preschoolers' causal inferences. Child Development 77 (2), 427–442. 1

Schulz, L. E., Standing, H. R., Bonawitz, E. B., Aug. 2008. Word, thought, and deed: the role of object categories in children's inductive inferences and exploratory play. Developmental Psychology 44 (5), 1266–1276. 4.4

Seed, A. M., Seddon, E. E., Greene, B. B., Call, J., Oct. 2012. Chimpanzee 'folk physics': bringing failures into focus. Philosophical Transactions of the Royal Society B: Biological Sciences 367 (1603), 2743–2752. 5.2

Shams, L., Seitz, A. R., Nov. 2008. Benefits of multisensory learning. Trends in Cognitive Sciences 12 (11), 411–417. 1

Shanahan, M., Oct. 2012. The brain's connective core and its role in animal cognition. Philosophical Transactions of the Royal Society B: Biological Sciences 367 (1603), 2704–2714. 3.2

Shanks, D. R. R., Mar. 2007. Associationism and cognition: human contingency learning at 25. Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology 60 (3), 291–309. 3.3

Shaw, J. M., 2008. Unifiying Perception and Curiosity. Ph.D. thesis, University of Rochester, Department of Computer Science, The College Arts and Sciences. Rochester, New York. 2

Shettleworth, S. J., May 1993. Where is the comparison in comparative cognition? Alternative research programs. Psychological Science 4 (3), 179–184. 1

Shettleworth, S. J., 1999. Cognition, Evolution, and Behavior. Oxford University Press, New York. 2.2

Sidman, M., Jul. 2000. Equivalence relations and the reinforcement contingency. Journal of the Experimental Analysis of Behavior 74 (1), 127–146. 5.1

Sloman, A., Dec. 2008a. The well-designed young mathematician. Artificial Intelligence 172 (18), 2015–2034. 1

Sloman, A., Jul. 2008b. Varieties of Meta-cognition in Natural and Artificial Systems Some pressures on design-space from niche-space I apologise For using Linux and L. Tech. rep., University of Birmingham, Cambridge, MA. 5.2

Sloman, A., 2010. The design-based approach to the study of mind (in humans, other animals, and machines), including the study of behaviour involving mental processes. In: Proceedings of the International Symposium on AI-Inspired Biology. pp. 87–94. 2.5

Sloman, A., Jan. 2011. What's information, for an organism or intelligent machine? How can a machine or organism mean? . In: Dodig-Crnkovic, G., Burgin, M. G. (Eds.), Information and Computation. World Scientific Publishing Co. Pte. Ltd., London, pp. 1–32. 1

Sloman, A., Chappell, J., 2005. Altricial self-organising information-processing systems. AISB Quarterly 121, 5–7. 3.4

Smith, J. D., Sep. 2009. The study of animal metacognition. Trends in Cognitive Sciences 13 (9), 389–396. 5.2

Smith, J. D., Ashby, F. G., Berg, M. E., Murphy, M. S., Spiering, B., Cook, R. G., Grace, R. C., Apr. 2011. Pigeons' categorization may be exclusively nonanalytic. Psychonomic Bulletin and Review 18 (2), 414–421. 3.2

Soto, F. A., Wasserman, E. A., Mar. 2012. Visual object categorization in birds and primates: integrating behavioral, neurobiological, and computational evidence within a "general process" framework. Cognitive, Affective and Behavioral Neuroscience 12 (1), 220–240. 3.2

Spelke, E. S., 2000. Core knowledge. American Psychologist 55 (11), 1233–1243. 4.1

Spirtes, P., Glymour, C. N., Scheines, R., 2000. Causation, Prediction, and Search. MIT Press. 3.3

Srinivasan, M., Gregory, R. L., 1992. How Bees Exploit Optic Flow: Behavioural Experiments and Neural Models [and Discussion]. Philosophical Transactions of the Royal Society B: Biological Sciences 337 (1281), 253–259. 3.1

Sterelny, K., Apr. 2007. Social intelligence, human intelligence and niche construction. Philosophical Transactions of the Royal Society B: Biological Sciences 362 (1480), 719–730. 2.5

Sussman, G. J., 1973. A Computational Model of Skill Acquisition. Ph.D. thesis, Elsevier Science Inc., Boston. 5.2

Taylor, A. H., Hunt, G. R., Medina, F. S., Gray, R. D., Jan. 2009. Do New Caledonian crows solve physical problems through causal reasoning? Proceedings of the Royal Society of London B: Biological Sciences 276 (1655), 247–254. 1, 5.3

Tecwyn, E. C., Thorpe, S. K. S., Chappell, J., Jan. 2012. What cognitive strategies do orangutans (*Pongo pygmaeus*) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles? Animal Cognition 15 (1), 121–133. 4.2

Tenenbaum, J. B., Griffiths, T. L., Kemp, C., Jul. 2006. Theory-based Bayesian models of inductive learning and reasoning. Trends in Cognitive Sciences 10 (7), 309–318. 4.4

Tenenbaum, J. B., Niyogi, S., 2003. Learning causal laws. In: Proceedings of the 25th annual meeting of the cognitive science society. Citeseer, pp. 1152–1157. 3.3

Thomas, R. K., Jun. 1996. Investigating cognitive abilities in animals: unrealized potential. Cognitive Brain Research 3 (3-4), 157–166. 1

Timmis, J., Hart, E., Hone, A., Neal, M., Robins, A., Stepney, S., Tyrrell, A., 2008. Immuno-engineering. In: Hinchey, M., Pagnoni, A., Rammig, F., Schmeck, H. (Eds.), IFIP International Federation for Information Processing. Springer, Boston, MA, pp. 3–17. 1

Toates, F. M., 1983. Exploration as a motivational and learning system: a cognitive incentive view. In: Archer, J., Birke, L. I. A. (Eds.), Exploration in animals and humans. Van Nostrand Reinhold, Berkshire, England, pp. 55–71. 1

Urcuioli, P. J., Nov. 2008. Associative symmetry, antisymmetry, and a theory of piegons' equivalence-class formation. Journal of the Experimental Analysis of Behavior 90 (3), 257–282. 5.1

Vermeulen, N., Mermillod, M., Godefroid, J., Corneille, O., Sep. 2009. Unintended embodiment of concepts into percepts: sensory activation boosts attention for same-modality concepts in the attentional blink paradigm. Cognition 112 (3), 467–472. 3.2

Visalberghi, E., Tomasello, M., 1998. Primate causal understanding in the physical and psychological domains. Behavioural Processes 42 (2-3), 189–203. 1

von Bayern, A. M. P., Heathcote, R. J., Rutz, C., Kacelnik, A., Dec. 2009. The role of experience in problem solving and innovative tool use in crows. Current Biology 19 (22), 1965–

1968. 2.5

Wasserman, E. A., Castro, L., Freeman, J. H., 2012. Same-different categorization in rats. Learning and Memory 19 (4), 142–145. 3.2

Wasserman, E. A., Young, M. E., Jan. 2010. Same-different discrimination: the keel and backbone of thought and reasoning. Journal of Experimental Psychology: Animal Behavior Processes 36 (1), 3–22. 3.2

Watanabe, S. S., Sakamoto, J. J., Wakita, M., Mar. 1995. Pigeons' discrimination of paintings by Monet and Picasso. Journal of the Experimental Analysis of Behavior 63 (2), 165–174. 3.2

Webb, B., Dec. 2001. Can robots make good models of biological behaviour? Behavioral and Brain Sciences 24 (6), 1033–50– discussion 1050–94. 1

White, R. W., 1959. Motivation reconsidered: The concept of competence. Psychological Review 66 (5), 297–333. 1

Wills, A. J., Lea, S. E. G., Leaver, L. A., Osthaus, B., Ryan, C. M. E., Suret, M. B., Bryant, C. M. L., Chapman, S., Millar, L., Nov. 2009. A comparative analysis of the categorization of multidimensional stimuli: I. Unidimensional classification does not necessarily imply analytic processing; evidence from pigeons (*Columba livia*), squirrels (*Sciurus carolinensis*), and humans (*Homo sapiens*). Journal of Comparative Psychology 123 (4), 391–405. 3.2

Wilz, K. J., Bolton, R. L., 1971. Exploratory behavior in response to the spatial rearrangement of familiar stimuli. Psychonomic Science 24 (3), 117–118. 2.1

Wimpenny, J. H., Weir, A. S., Clayton, L., Rutz, C., Kacelnik, A., 2009. Cognitive processes associated with sequential tool use in New Caledonian crows. PloS One 4 (8), e6471–e6471. 2.2.2

Wing, A. M., Lederman, S. J., Dec. 1998. Anticipating load torques produced by voluntary movements. Journal of Experimental Psychology: Human Perception and Performance 24 (6), 1571–1581. 3.1

Wright, A., Katz, J. S., Jun. 2006. Mechanisms of same/different concept learning in primates and avians. Behavioural Processes 72 (3), 234–254. 3.2

Zucca, P., Milos, N., Vallortigara, G., Apr. 2007. Piagetian object permanence and its development in Eurasian jays (*Garrulus glandarius*). Animal Cognition 10 (2), 243–258. 4.1

Glossary

Abnormal Behaviour 125
Occurs in captive animals and a general indicator of poor welfare. Includes any behaviour that is inappropriately repetitive in goal or motor pattern, often functionless, maladaptive or self-injurious (Garner et al., 2006).

Abstraction 226
The process by which first principles are used to deduce higher concepts.

Affordances 4
All action possibilities present in the environment (e.g. different object properties), objectively measurable and independent of the individual's ability to recognise them, but always in relation to the actor and therefore dependent on their capabilities (Gibson, 1977). For instance, a pencil affords writing, or a piece of paper affords ripping.

Altricial Development 161
When a species is dependent on its parents for an extended period of time, as it was born/hatched in a developmental state where it could not yet survive by itself. Human babies are quite an extreme example of this, where children are dependent on their parents for at least 12 years. The opposite is known as 'precocial development' and includes animals like deer, which can fully locomote around within moments of birth.

Anthropocentrism 163
The regard that humans are the central or most important element of existence, especially in comparison with other animals.

Anticipatory Grip Forces 169
Dextrous object manipulation needs precise digit positioning and forces, which often are estimated according to sensory feedback and processing delays; these initial grip forces exerted on an object are the 'anticipatory grip forces'.

Associative Learning 3
A simple learning mechanism, where an animal realises a causal relationship between two stimuli. This can be through 'classical conditioning' or 'operant conditioning'. In the latter, reward or punishment is used to modify the occurence/type of a behaviour (action-outcome association), whereas in the former, a stimulus-outcome association is strengthened.

Bayesian Network 4
A type of statistical model that uses a directed acyclic graph to represent a set of random variables and their conditional dependencies.

Bill Tip Organ 10
The region found near the tip of a bill in several types of birds that forage by remote touch (e.g. shorebirds), which has a high density of touch receptors known as the Herbst and Grandry corpuscles. These are embedded in pits near the bill surface.

Binocular Visual Field 10
The region of the world external to the animal that both eyes can see. In other words, where each eye's visual field ('monocular' field) overlap, usually at the front of the animal.

Bowers 161
In referring to the structure created by bowerbirds (Ptilonorhynchidae) for courtship displays. They are made out of sticks (sometimes arranged around a sapling) and decorated with brightly coloured objects.

Causal Inferences 213
Also referred to as 'inferential reasoning'; the ability to infer the underlying cause to perceived (often incomplete) sensory information. In the other words, the ability to associate a perceived event with an imagined event based on causal or physical reasoning. One example is to infer what is going on by exclusion of the various possibilities.

Causal Learning 272
The process of gathering and storing information about the causes of the events and how the physics of the world works (e.g. gravity, continuity, or different object properties).

Causal Understanding or Causal Reasoning 3
The knowledge or understanding or ability to reason about the relationship/mechanism between the cause and effect of events in the environment. In other words, some understanding about how the physics of the world work.

Celestial Hemisphere 11
If one imagines a bird's head in the middle of a sphere, the celestial

hemisphere refers to the whole region above the bird's head. If there was a horizontal line drawn through the middle of the sphere and the middle of one of the bird's eye, this would be the region above this horizontal line, from straight out in front of them, to straight out behind them.

Centre-of-gravity 168
Though subtly different, also known as the 'centre-of-mass'; referring to average weighted location of all of the mass of a physical body (/object), or group of bodies. It does not necessarily coincide with the geometric centre of the body. Balance of an object is attained when the vertical line from the centre-of-gravity of the object is within the foundation of support with minimal postural sway.

Cognitive Flexibility 121
Refers to an ability to explicitly think and reason about the past, present or future abstractly or adaptively. The individual is not restricted to specific circumstances or specific environments. For example 'learning generalisation'; an individual can generalise their knowledge about a previous event or object property to a novel, but similar event or property. The individual can also 'abstract concepts' from a collection of information or learning events.

Concepts 231
Quite abstract knowledge about the world, combining different bits of related information into one. For instance, 'above' and 'below' are opposite concepts, as are 'same' or 'different'. Thus often involved in the categorisation process.

Configurational Shape 207
When an individual perceives an object's configurational shape, he/she perceives the outline of the object's shape, or the geometric organisation of its contours, as separate from its surroundings.

Construct Knowledge 226
The process of learning about the world, to build/form internal representations within one's brain, usually through active interaction and testing of the surrounding environment or nearby objects.

Cross-modal Interaction 29
The use of the different senses, to allow the characteristics of one sensory modality to be transformed into information for another sensory modality. Similar to 'multi-modal interaction' uses each modality to transmit a different form of information. This means that representation of this information in the brain may be amodal (non-sensory).

Cyclopean Field 14
The total visual field of an animal, produced by the combination of both monocular fields.

Cyclopean Projection Centre 15
If one treats the two eyes as if they are behaving as a single eye situated in the centre of the forehead. From here, the projection is from the two separate retinal points: the mid-point of the line joining the centres of the pupils.

Designer-based Approach 5
Inspired by the field of artificial intelligence; where biologists should think like programmers to reason through the environmental constraints the organism is faced with and consider how it solves them – consider what the 'requirements' are of the environment. Then biologists should analyse the different possible designs that could fulfil these requirements, comparing the results with the actual designs revealed by observing the real animals (Chappell et al., 2012).

Ecological Niche 113
Can point to the environment, or a way of life, of a particular species; or can point to the environment of a particular individual. It refers to how an animal (/population) responds to various ecological factors within its habitat (resource distribution, predators, competition) and how it alters those same factors. It will depend on how the animal has evolved, what anatomy or sensorimotor systems it possesses, but also its various individual abilities. A niche can also refer to the set of affordances for a particular animal (Chemero, 2003).

Environmental Enrichment 123
Results in an improvement in the biological functioning (in health or lifetime reproductive success) of captive animals resulting from modifications to their environment (Newberry, 1995).

Exploitation 122
Half of an optimality trade-off in decision-making (the other half is exploration). The individual has to decide between optimising its decisions based on existing knowledge ('exploitation'), and acquiring new knowledge in the hope of finding something useful ('exploration'; Cohen et al., 2007).

Exploration Domains 227
A specific group of affordances or processes integrated into a single internal representation, perhaps within a single neural structure of some sort. They are related by their similar function. Karmiloff-Smith (1995) had a similar term: 'micro-domains'. Note the opposite term would be a general-purpose representation that incorporates all information into one place.

Exploratory Approach Phase 27
The first of the two phases in exploration, preceding the 'exploratory manipulation phase'. The locomotory approach towards an object,

which, once identified, the animal needs to gain more information about. This is usually from a distance of over 10 cm from the target object until within grasping distance (e.g. 5 cm between parrot and toy). The predominant sense used in this phase is likely vision.

Exploratory Learning or Exploration 2
Perceptual and motor interactions with objects, with no immediate benefit/function, except to gather environmental information, sometimes in parallel with another activity, including problem solving by goal-directed action.

Exploratory Manipulation Phase 28
The second of the two phases in exploration, after the 'exploratory approach phase'. The manipulation and physical interaction with the target object to gain information about it. This commences from when the target is within grasping distance (e.g. 5 cm between parrot and toy). The predominant sense used in this phase is likely touch, at least in parrots.

Exploratory Style 162
Similar to a personality trait; within a population, there is usually a lot of individual variation in exploratory styles. A given individual usually uses the same style (suite of behaviours) over a long period of time, and behavioural reactions are often correlated across different environmental situations. Exploratory style broadly reflects whether an individual is shy or confident in its exploratory behaviour. For instance, one measure of an exploratory style is the likelihood for an individual to approach a novel object (e.g. Verbeek et al, 1994).

Extractive Foraging 11
A type of foraging, where the food item is extracted in some way from inside something else, such as a nut from its shell, but it could also be extracting roots from the soil. Parrots are a prime example of extractive foraging, using their hard hooked bills to break into nuts.

Filter Feeders 10
Refers to any birds that forage primarily by straining suspended matter and food particles from water, typically by passing it over a specialised structure, such as with mallard ducks or flamingoes.

Footedness 33
When performing a particular behaviour (e.g. kicking a ball, or, in a parrot's case, manipulating an object), the individual prefers to use one foot more than the other.

Functional or Causal Cues 151
Refers to cues in the external environment that give the observer information about the object's affordances, such as what it can cause

when acted upon, or what it can be used for. Related to its physical properties or affordances, as well as its possible goals when acted upon. For example, the corners on a cube suggest (without touching it) that it cannot roll like a ball can (with just curved edges). On the other hand, colours are 'non-functional' or 'aesthetic' cues and often do not give any information about an object's affordances.

Goal-directed Action 2
Refers to quite conscious drives for a behaviour, where the individual is aware of what it wants to accomplish, rather than implicit motivations. For instance, finding a food item, or solving a particular problem.

Haptic Exploration 26
Any information gathered passively or actively (i.e. unconsciously or not) through inputs from receptors embedded in the skin (i.e. 'touch'), and/or in the muscles, tendons and joints (i.e. 'proprioception' such as through grasping). For instance, an individual can obtain haptic (or 'tactile') cues about an object's shape not only from skin deformation and limb displacements, but also from the temporal changes in net forces resulting from friction between the skin and the explored surface (Lederman & Klatzky, 1993; Smith et al., 2009; Schneider, 2011).

Information 1
This thesis largely refers to the everyday use of the word, referring to semantic content that is about something that actually exists or could exist (Sloman, 2011).

Inhibitory Control 272
Nerve impulses that dampen or stop certain responses or activities. At the more behavioural level, it can refer to the inability to stop impulsive, prepotent responses to a particular environmental stimulus, particularly if extensively reinforced behaviour beforehand.

Ipsilateral 62
When something is on the same physical side as something else (e.g. left eye with left foot), as opposed to 'contralateral', when they are on opposite sides.

Juvenescence 11
Basically childhood, or the period of time from hatching/birth to sexual maturity.

Kepler-Poinsot Polyhedron 182
Plain Layouty of the four regular star-shaped polyhedra, which are created by stellating either a regular convex dodecahedron, or a regular convex icosahedron. They differ from these regular convex polyhedra by having faces in the shape of pentagrams. The simplest regular star is the 'small stellated dodecahedron'.

Keratin 12
A family of fibrous, structural proteins, often continually growing, such as those found in nails, hooves or bird beaks.

Kinetics 216
The relationship between the motion of objects and the causes (forces and torques). A related concept is 'kinematics', which is more concerned with the movement of the points of objects (or groups of objects) without considering the causes. Kinetics is surmised from kinematics by the presence of mass.

Knowledge 228
The representation of information about the environment in the brain with associated concepts (Sloman, 2011).

Latent Learning 122
The gathering of information when there is no apparent immediate or future reward, where there is no overt response in the short term.

Lateralisation 25
The division of the two brain hemispheres ('cerebral lateralisation'), which manifests itself as side biases in motor behaviour (e.g. 'handedness', 'footedness', or 'motor lateralisation') or in a preference for stimulus perception on the left or right side (e.g. with a particular eye, 'visual lateralisation').

Maxilla 11
The upper 'jaw' of a bird's bill, as opposed to the 'mandible', which is the lower jaw.

Mechanoreceptors 12
Touch receptors that specifically respond to mechanical pressure or distortion, such as Herbst or Grandry corpuscles.

Mesopallium 11
In a bird's brain, lower part of old hyperstriatum or the middle part of the pallium. The pallium is thought to be the avian equivalent of the mammal cortex (Jarvis et al., 2005).

Monocular Field 14
The patterns and the changes of pattern of light perceived by the retina (or transformations of a small bounded cone of the optic array), resulting in stimuli for the control of locomotion relative to the objects of the environment (Gibson, 1958). As opposed to for instance a classical control or cybernetics control approach using closed-loop, feedback mechanisms for determining the motor aspects of locomotion, away from vision.

Naris 32
Plural is 'nares'; the nostril of a bird, located at the top of the maxilla

(bird's upper mandible). Can refer to the nostrils of other vertebrates too.

Natural Activity Levels or Pattern 123
The frequency or sequence of different behaviours performed by an animal each day in the wild. One can produce an 'activity budget' from this information, which illustrates the percentage of time the animal spent exploring/grooming/courting/feeding etc. during the day.

Neophilia 3
The love of new things; the opposite of 'neophobia'. Note this is a separate personality trait to 'exploratory'.

Object Permanence 274
The understanding that objects continue to exist, even if they are not being currently viewed, touched or heard.

Object Relations 228
The causal understanding of how multiple objects interact and influence each other's behaviour. For instance, if a supporting block is taken away, the block stacked on top of it will fall. Another example is understanding how cogs turn in relation to each other.

Online 280
The point at which different cognitive (or motor) capacities are 'turned on' by the genes at a certain stage in development.

Opthalmoscope 15
An hand-held instrument to view eyes, about the size of a small torch, with a light and several lenses that can magnify the eye up to about 15 times. Best viewed in a darkened room.

Optic Axis 16
The line connecting the anterior and the posterior poles of the eye. Where optic axes project out of each eye, is thought to be the region of greatest visual acuity in the visual field.

Optic Flow Field 39
The field of view produced by relative motion between the individual and the surrounding environment, resulting in a pattern of apparent motion of objects, surfaces, and edges., ... 69
The field of view produced by relative motion between the individual and the surrounding environment, resulting in a pattern of apparent motion of objects, surfaces, and edges., ... 103
The field of view produced by relative motion between the individual and the surrounding environment, resulting in a pattern of apparent motion of objects, surfaces, and edges.

Pecten 16
A pigmented area of the avian retina near the optic nerve that is non-sensory and full of blood vessels, so it is thought to nourish the retina and control the pH levels of the viterous body (i.e. the clear gel that fills the eye). It thus creates a small blind area in the visual field.

Perseveration 148
The repetition of a certain behavioural response despite the absence of the related stimulus.

Physical Rules 230
An internal representation of rules for how the physics of the world work, where there are environmental constants. A framework of these rules is likely encoded into the genes, upon which individuals can build on with learning and experience. For example, gravity (all things must fall), or object solidity (no two solid things can go through each other).

Physical Understanding 221
Similar to 'causal understanding'; some level of knowledge of how the physics of the world works. Also known as 'folk physics'.

Play 75
Play is a form of exploration, but it is not necessarily for gathering information. Instead, it is more related to the current or future benefits of this quite directionless/goaless behaviour, except for the feeling of fun in doing it.

Probabilistic Learning 4
To learn about the world using statistical mechanisms, calculating the different exact probabilities of different possibilities, e.g. through Bayesian networks.

Proprioception 66
The perception of where one's own body and each of its parts are and how they are moving through space, from information received in sensory receptors mainly embedded in muscles, tendons, joints, and the inner ear.

Psittacine 5
Collectively refer to the birds found in the order Psittaciformes, which includes the common and typical 'true' parrots (Psittacoidea), crested parrots such as cockatoos (Cacatuoidea), and the more evolutionarily diverged or ancient New Zealand parrots (Strigopoidea). Note that the term 'psittacids' just refer to the true parrots.

Purkinje Images 16
Reflections from the cornea and the lens anterior surface of the eye. They are used by some eye-tracking devices to measure the position of the eye.

Recognition Memory 211
The ability to consciously recognise previously experienced events, objects or other individuals, by comparing and matching the current (re-experienced) event to the stored representation.

Regular Polyhedron 182
A three-dimensional, geometric shape, with flat surfaces and straight edges. The plural is 'polyhedra'. This includes 'Platonic solids', which are regular, congruent, convex polyhedra, where the same number of faces meet at each vertex.

Representation (Internal) 226
Inspired by the field of artificial intelligence, where biologists should think like programmers to reason through the environmental constraints the organism is faced with and how they solve it – consider what the 'requirements' are of the environment. Then biologists should analyse the different possible designs which could fulfil these requirements, comparing the results with the actual designs revealed by observing the real animals (Chappell et al., 2012).

Retinal Field 15
The functional visual field, encompassing what the bird can actually see, as opposed to the 'optical field', which the retina does not always serve the entirety of, especially in the periphery. For instance, in short-toed eagles (*Circaetus gallicus*) it is possible to see into the eye through the pupil at the frontal margin of the optical field and thus gain the impression of a wide binocular field. However, there is not any retina serving that part of the optical field, i.e., there is a 'blind optical margin' (Martin, 2009).

Rhamphotheca 12
The outer, hard keratinised epidermis or layer that the covers the beak of birds.

Sensorimotor 64
This term refers to both the sensory and motor functions of an animal or to the nerves controlling them. Note that strictly information gathered through the senses and that processed through the motor system are separate entities. As in behavioural experiments, it is generally difficult to separate these two facets, therefore we collectively refer to both as 'sensorimotor'. For instance, the parrot bill provides both a sensory function, in receiving haptic information through its bill tip organ, and a motor function, in its dextrous manipulation of objects.

Somatosensory 12
Refers to sensory information that includes the perception of touch, temperature, proprioception (body position), and nociception (pain).

Somatosensory receptors can be found in the skin, skeletal muscles, bones, joints, internal organs and the cardiovascular system.

Stellation 182
The process of creating new shapes in n number of dimensions. In two dimensions this creates 'polygons'; and in three dimensions this creates 'polyhedra'. This usually means extending elements like edges or faces (often in a symmetrical way) until they meet each other again.

Stereopsis 103
Perception of depth resulting from the brain integrating the receptions from two slightly different projections of the visual scene onto the retinas of two eyes, especially where their fields of view overlap.

Stereotypical Behaviour 125
Occurs in captive animals and a general indicator of poor welfare. Includes any behaviour that is a sequence of movements that are repeatedly identically. They are inappropriate and lack any function or goal (Garner et al., 2006).

Synovial Joint 11
A joint that permits more or less free motion, by the union of the bony elements, surrounded by an articular capsule (i.e. envelope of white fibrous tissue and a secreting layer), enclosing a cavity lined by a synovial membrane.

Tactile Probers 10
Refers to any birds that forage primarily by remote touch with their bill tip organ. For instance, shorebirds probe with their bills into soft mud to sense for vibrations from invertebrate prey embedded somewhere in the substrate.

Tetrachromacy 206
A tetrachromat is an individual who has four separate perception pathways for processing colour, such as four types of 'cone cells' in the eye, each of which have different absorption spectrum for seeing different parts of the colour spectrum. Humans are largely trichromats (three pathways). Conversely, many birds are tetrachromats – able to see into the ultraviolet spectrum, while we cannot.

Torque 169
The momentum of a force rotating about an axis.

Uncertainty 122
When an individual faces ambiguous or incomplete information, whether externally from what is front of them in the environment, or internally from erroneous memory. See Inglis et al. (2001) for more information.

Vertex 182
In Euclidean geometry, this term refers to a point, where the corners of geometric shapes intersect.

Vestibular System 37
The sensory system that provides information about rotational movements and linear acceleration to aid in balance and movement. It is tightly integrated with eye movements (for clear vision) and the muscles that control posture (to keep the animal upright).

Vibrissa 67
In mammals, this refers to long, stiff hairs that project from an animal's snout and/or brow. In birds, this refers to specialised feathers that grow around the bill of insectivorous individuals. Both serve as tactile organs.

Visual Acuity 22
Sharpness of vision, or the eye's ability to distinguish object details and shape in the direct line of sight. Often measured using the smallest identifiable object that can be seen at a specified distance.

Visual Field 10
The total area in which objects and other features of the external world that can be seen by the animal, including those in the periphery, while the eyes focus on a central point. An animal's visual field essentially governs what can influence its behaviour from moment to moment.

Whisking Behaviour 67
Rodents sweep their facial whiskers back and forth in a rhythmic way when moving about the world (Grant et al., 2009).

Zygodactyl 11
Describes a type of foot, where two toes are facing forward and two toes are facing backward, thought to be adapted for climbing birds like woodpeckers or cuckoos (Smith, 1975). As opposed to the more common foot found in birds, 'anisodactyl', three toes forward, two toes back, such as in Passeriformes.

References

A

Abou-Ismail, U. a., Burman, O. H. P., Nicol, C. J., and Mendl, M. (2010). The effects of enhancing cage complexity on the behaviour and welfare of laboratory rats. *Behavioural Processes*, **85**(2):172–180. II

Adolph, K. E., Joh, A. S., and Eppler, M. A. (2010). Infants' perception of affordances of slopes under high- and low-friction conditions. *Journal of Experimental Psychology: Human Perception and Performance*, **36**(4):797–811. 6.4.1

Alaerts, K., Swinnen, S. P., and Wenderoth, N. (2009). Interaction of sound and sight during action perception: Evidence for shared modality-dependent action representations. *Neuropsychologia*, **47**(12):2593–2599. 3.4.3

Albert, D. J. and Mah, C. J. (1972). An examination of conditioned reinforcement using a one-trial learning procedure. *Learning and Motivation*, **3**:369–388. II

Alderton, D. (2005). *The Ultimate Encyclopedia of Caged and Aviary Birds*. Southwater, Horsham. I, 3.2.1

Amsel, E. and Brock, S. (1996). The development of evidence evaluation skills. *Cognitive Development*, **11**(4):523–550. 6.4.6

Archer, J. and Birke, L. I. A. (1983). *Exploration in animals and humans*. Van Nostrand Reinhold, Workingham. 1, 3.4.3, II, III

Arenas, A. and Farina, W. M. (2012). Learned olfactory cues affect pollen-foraging preferences in honeybees, Apis mellifera. *Animal Behaviour*, **83**(4):1023–1033. II

ARKive (2010). Image search: 'parrot flight climb'. http://www.arkive.org/. 2.4.3, 3.1.1

Arriola-Rios, V. E., Demery, Z. P., Wyatt, J., Sloman, A., and Chappell, J. (2013). Salient Features and Snapshots in Time: An Interdisciplinary Perspective on Object Representation. In Dodig-Crnkovic, G. and Giovagnoli, R., editors, *Studies in Applied Philosophy, Epistemology and Rational Ethics: Computing Nature*, pages 171–184. Springer-Verlag, Berlin, Heidelberg. 3.4.3, II, 5.4.1, 5.4.2, 5.4.5, III, III, III, 6.4.4, 6.4.5, 6.4.6, 6.4.6, 6.4.6, 7.4.1, 7.4.2, 7.4.3, 7.4.4, 7.4.5, 7.4.6, 8, E, E.1

Arriola-Rios, V. E. and Savage, J. (2007). Knowledge Acquisition and Automatic Generation of Rules for the Inference Machine CLIPS. In Gelbukh, A. F. and Kuri Morales, A. F., editors, *MICAI 2007: Advances in Artificial Intelligence, 6th Mexican International Conference on Artificial Intelligence*, pages 725–735, Aguascalientes, Mexico. Springer. 6.4.5

Athan, M. and Deter, D. (2009). *Guide to the Senegal Parrot and Its Family*. Barron's Educational Series, London. I, 3.2.1

Auersperg, A., von Bayern, A. M. P., Gajdon, G. K., Huber, L., and Kacelnik, A. (2011). Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. *PloS One*, **6**(6):e20231. II, III

Augustsson, H. H., Dahlborn, K. K., and Meyerson, B. J. B. (2005). Exploration and risk assessment in female wild house mice (*Mus musculus musculus*) and two laboratory strains. *Physiology and Behaviour*, **84**(2):13–13. II

Aust, U. U., Range, F., Steurer, M., and Huber, L. (2008). Inferential reasoning by exclusion in pigeons, dogs, and humans. *Animal Cognition*, **11**(4):587–597. 6.4.3

Avargues-Weber, A., Dyer, A. G., and Giurfa, M. (2011). Conceptualization of above and below relationships by an insect. *Proceedings of the Royal Society of London B: Biological Sciences*, **278**(1707):898–905. II

Avni, R. R., Tzvaigrach, Y. Y., and Eilam, D. D. (2008). Exploration and navigation in the blind mole rat (*Spalax ehrenbergi*): global calibration as a primer of spatial representation. *Journal of Experimental Biology*, **211**(Pt 17):2817–2826. 3.4.3

B

Baillargeon, R. (2002). The Acquisition of Physical Knowledge in Infancy: A Summary in Eight Lessons. In Goswami, U., editor, *Handbook of Childhood Cognitive Development*, pages 47–83. Blackwell Publishers Ltd. 6.4.6, 7.4.2

Baillargeon, R. R. and DeVos, J. J. (1991). Object permanence in young infants: further evidence. *Child Development*, **62**(6):1227–1246. 7.4.3

Bajcsy, R. (1989). Active Perception and Exploratory Robotics. Technical report, University of Pennsylvania, School of Engineering and Applied Science, Department of Computer and Information Science, Pennsylvania. 1

Baldwin, D. A., Markman, E. M., and Melartin, R. L. (1993). Infants' ability to draw inferences about nonobvious object properties: evidence from exploratory play. *Child Development*, **64**(3):711–728. 6.4.6, 6.4.6

Bard, K. A. (1995). Sensorimotor cognition in young feral orangutans (*Pongo pygmaeus*). *Primates*, **36**(3):297–321. 3.4.3, III, C.1

Barsky, P. I. (2010). Environment, genes, and experience: lessons from behavior genetics. *Journal of Physiology*, **104**(5):243–252. II

Beck, B. (1980). *Animal tool behavior: the use and manufacture of tools by animals*. Garland series in ethology. Garland STPM Pub. III

Beck, S. R., Robinson, E. J., and Freeth, M. (2008). Can children resist making interpretations when uncertain? *Journal of Experimental Child Psychology*, **99**(4):252–270. II, 5.4.3, 7.4.3, 8

Bekoff, M. (1975). Animal play and behavioral diversity. *American Naturalist*, **109**(969):601–603. II

Bekoff, M. and Byers, J. A. (1998). *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. Evolutionary, Comparative and Ecological Perspectives. Cambridge University Press, Cambridge, UK. 1, II, III, 6.4.5

Belsky, J. and Most, R. K. (1981). From exploration to play: A cross-sectional study of infant free play behavior. *Developmental Psychology*, **17**(5):630–639. 6.4.1

Bergtold, W. H. (1906). Concerning the Thick-Billed Parrot. *Auk*, **23**(4):425–428. 2.4.3

Berkhoudt, H. (1979). The Morphology and Distribution of Cutaneous Mechanoreceptors (Herbst and Grandry Corpuscles) in Bill and Tongue of the Mallard (*Anas Platyrhynchos L.*). *Netherlands Journal of Zoology*, **30**(1):1–34. I, 2.2.3, 2.3.2, 4.4.2

Berlyne, D. E. (1950). Novelty and curiosity as determinants of wild and laboratory rats. *British Journal of Psychology*, **41**:68–80. 6.4.2

Berlyne, D. E. (1960). *Conflict, arousal, and curiosity.* McGraw-Hill Book Company, New York, NY, US. 1, III, 6.4.3, 6.4.6, 6.4.6

Bertram, B. C. R. (1978). Living in groups: predators and prey. In Krebs, J. R. and Davies, N. B., editors, *Behavioural Ecology*, pages 64–96. Blackwell Science Ltd, Oxford. 3.4.3

Bhagavatula, P., Claudianos, C., Ibbotson, M., and Srinivasan, M. (2009). Edge detection in landing budgerigars (*Melopsittacus undulatus*). *PloS One*, **4**(10):e7301. III, 6.4.1

Birdslife International (2011). Psittacines: Parrots & Cockatoos. http://www.birdlife.org/datazone/species. 1

Bisazza, A., Lippolis, G., and Vallortigara, G. (2001). Lateralization of ventral fins use during object exploration in the blue gourami (*Trichogaster trichopterus*). *Physiology and Behaviour*, **72**(4):575–578. 3.4.3, 4.4.3

Bisazza, A., Rogers, L. J., and Vallortigara, G. (1998). The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neuroscience and Biobehavioral Reviews*, **22**(3):411–426. 4.4.3

Bluff, L. A., Troscianko, J., Weir, A. S., Kacelnik, A., and Rutz, C. (2010). Tool use by wild New Caledonian crows *Corvus moneduloides* at natural foraging sites. *Proceedings of the Royal Society of London B: Biological Sciences*, **277**(1686):1377–1385. III

Bluff, L. A., Weir, A. S., Rutz, C., Wimpenny, J. H., and Kacelnik, A. (2007). Tool-related cognition in new Caledonian crows. *Comparative Cognition and Behavior Reviews*, **2**(1):1–25. III

Blumstein, D. T., Daniel, J. C., and Evans, C. S. (2007). *Quantifying behavior the JWatcher way*. Sinauer Associates, London. 4.2.3, 5.2.3, 6.2.3, C.1, C.2, C.3

Bock, W. J. and Miller, W. D. W. (1959). *The Scansorial Foot of the Woodpeckers, with Comments on the Evolution of Perching and Climbing Feet in Birds*. American Museum Novitiates. American Museum of Natural History, New York. 3.4.3

Bonawitz, E. B., Fischer, A., and Schulz, L. E. (2012a). Teaching 3.5-year-olds to revise their beliefs given ambiguous evidence. *Journal of Cognition and Development*, **13**(2):266–280. II, 7.4.3

Bonawitz, E. B., van Schijndel, T. J. P., Friel, D. D., and Schulz, L. E. (2012b). Children balance theories and evidence in exploration, explanation, and learning. *Cognitive Psychology*, **64**(4):215–234. 6.4.4

Bonser, R. (1999). Branching out in locomotion: the mechanics of perch use in birds and primates. *Journal of Experimental Biology*, **202**(Pt 11):1459–1463. 2.4.3, 3.4, 6.4.5

Bonser, R. and Rayner, J. (1996). Measuring leg thrust forces in the common starling. *Journal of Experimental Biology*, **199**(2):435. 2.4.3, 3.4

Boon, W. M., Kearvell, J. C., Daugherty, C. H., and Chambers, G. K. (2001). *Molecular Systematics and Conservation of Kakariki (*Cyanoramphus *spp.)*. Department of Conservation, London. 4.2.1, 5.2.1, III, 6.2.1

Bourgeois, K., Khawar, A. W., Neal, S. A., and Lockman, J. (2005). Infant manual exploration of objects, surfaces, and their interrelations. *Infancy*, **8**(3):233–252. III, 6.4.1, 6.4.5

Brooks, D. I. and Wasserman, E. A. (2010). Contrasting object-based and texture-based accounts of same/different discrimination learning with trial-unique stimuli. *Journal of Experimental Psychology: Animal Behavior Processes*, **36**(1):158–163. 6.4.1

Brown, C. and Magat, M. (2011a). Cerebral lateralization determines hand preferences in Australian parrots. *Biology Letters*, **7**(4):496–498. 2.4.1, 2.4.2, 2.4.3, 3.4.3, 3.4.3, 3.4.3, 4.4, 4.4.3, 3, 4.4.3

Brown, C. and Magat, M. (2011b). The evolution of lateralized foot use in parrots: a phylogenetic approach. *Behavioral Ecology*, **22**(6):1201–1208. 3.4.3, 4.2.6, 4.4.3

Bryant, P. E. P., Jones, P. P., Claxton, V. V., and Perkins, G. M. (1972). Recognition of shapes across modalities by infants. *Nature*, **240**(5379):303–304. 6.4.1

Brydges, N. M. and Braithwaite, V. A. (2008). **Measuring Animal Welfare: What Can Cognition Contribute?** *Annual Review of Biomedical Sciences*, **10**(0). 5.4.4

Brydges, N. M., Leach, M., Nicol, K., Wright, R., and Bateson, M. (2011). Environmental enrichment induces optimistic cognitive bias in rats. *Animal Behaviour*, **81**(1):169–175. II, 6.4.3

Buchsbaum, D. D., Bridgers, S. S., Weisberg, D. D. S., and Gopnik, A. (2012). The power of possibility: causal learning, counterfactual reasoning, and pretend play. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1599):2202–2212. 1, 6.4.6, 7.4.5

Bunzeck, N. N., Dayan, P., Dolan, R. J., and Duzel, E. (2010). A common mechanism for adaptive scaling of reward and novelty. *Human Brain Mapping*, **31**(9):1380–1394. 1, 3.4.3, 5.4.3

Bushnell, E. W. and Boudreau, J. P. (1993). Motor development and the mind: the potential role of motor abilities as a determinant of aspects of perceptual development. *Child Development*, **64**(4):1005–1021. 3.4.3, 4.4.2, III, 6.4.1, 6.4.3, 6.4.5, 6.4.6, 7.4.4

Byers, J. A. and Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *American Naturalist*, **146**(1):25–40. III

Byrne, R. W. and Bates, L. A. (2011). Cognition in the wild: exploring animal minds with observational evidence. *Biology Letters*, **7**(4):619–622. 1

C

Cacchione, T. and Call, J. (2010). Intuitions about gravity and solidity in great apes: the tubes task. *Developmental Science*, **13**(2):320–330. 6.4.3, 7.4.2

Cacchione, T., Call, J., and Zingg, R. (2009). Gravity and solidity in four great ape species (*Gorilla gorilla, Pongo pygmaeus, Pan troglodytes, Pan paniscus*): vertical and horizontal variations of the table task. *Journal of Comparative Psychology*, **123**(2):168–180. 7.4.2

Cacchione, T. and Krist, H. (2004). Recognizing impossible object relations: intuitions about support in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **118**(2):140–148. 6.4.3

Callebaut, W. and Rasskin-Gutman, D. (2005). *Modularity: Understanding The Development And Evolution Of Natural Complex Systems*. MIT Press, London. 7.4.4

Campolo, D., Maini, E. S., Patane, F., Laschi, C., Dario, P., Keller, F., and Guglielmelli, E. (2009). Design of a sensorized ball for ecological behavioral analysis of infants. In *2007 IEEE International Conference on Robotics and Automation*, pages 1529–1534. 8

Carruthers, P. (2006). *The Architecture of the Mind: Massive Modularity and the Flexibility of Thought: massive modularity and the flexibility of thought*. Clarendon Press, London. 7.4.4

Cartmill, M. (1985). Climbing. In Hildebrand, M., Bramble, D. M., Liem, K. F., and Wake, D. B., editors, *Functional Vertebrate Morphology*, pages 77–88. Harvard University Press, Cambridge, MA. 2.4.3, 3.4

Caruso, D. A. (1993). Dimensions of quality in infants' exploratory behavior: Relationships to problem-solving ability. *Infant Behavior and Development*, **16**(4):441–454. III, 6.4.6

Casey, M. B. (2005). Asymmetrical hatching behaviors: the development of postnatal motor laterality in three precocial bird species. *Developmental Psychobiology*, **47**(2):123–135. 2.4.1, 2.4.2, 2.4.3, 3.4.3

Chappell, J., Demery, Z. P., Arriola-Rios, V. E., and Sloman, A. (2012). How to build an information gathering and processing system: lessons from naturally and artificially intelligent systems. *Behavioural Processes*, **89**(2):179–186. 2.4.2, 3.4.3, 4.4.2, II, III, III, III, 6.4.5, 6.4.6, 6.4.6, 6.4.6, 6.4.6, 7.4.4, 7.4.5

Chappell, J. and Hawes, N. (2012a). Biological and artificial cognition: what can we learn about mechanisms by modelling physical cognition problems? *Philosophical Transactions of the Royal Society B: Biological Sciences*, pages 1–15. III

Chappell, J. and Hawes, N. (2012b). Biological and artificial cognition: what can we learn about mechanisms by modelling physical cognition problems using artificial intelligence planning techniques? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1603):2723–2732. 8

Chappell, J. and Kacelnik, A. (2002). Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, **5**(2):71–78. III

Chappell, J. and Sloman, A. (2007). Natural and Artificial Meta-Configured Altricial Information-Processing Systems. *International Journal of Unconventional Computing*, **2**(3):211–239. 1, II, III, 6.4.5, 6.4.6

Charusta, K., Dimitrov, D., Lilienthal, A., and Iliev, B. (2009). Extraction of grasp-related features by human dual-hand object exploration. In *Advanced Robotics, 2009. ICAR 2009. International Conference on*, pages 1–6. 6.4.1

Chemero, A. (2003). An outline of a theory of affordances. *Ecological Psychology*, **15**(2):181–195. 1

Chemero, A. and Heyser, C. J. (2005). Object Exploration and a Problem with Reductionism. *Synthese*, **147**(3):403–423. 1

Chevalier-Skolnikoff, S. (1977). A Piagetian model for describing and comparing socialization in monkey, ape, and human infants. In *Primate biosocial development: Biological, social, and ecological determinants*, pages 159–187. Garland Publishing, London. III

Chittka, L. and Jensen, K. (2011). Animal Cognition: Concepts from Apes to Bees. *Current Biology*, **21**(3):R116–R119. 1

Chittka, L., Rossiter, S. J., Skorupski, P. P., and Fernando, C. C. (2012). What is comparable in comparative cognition? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1603):2677–2685. 7.4.5

Clark, F. E. (2011). Great ape cognition and captive care: can cognitive challenges enhance well-being? *Applied Animal Behaviour Science*, **135**(1-2):1–12. 5.4.4, III

Clayton, N. S. and Krebs, J. R. (1994). Lateralization and unilateral transfer of spatial memory in marsh tits: are two eyes better than one? *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology*, **174**(6):769–773. 3.4.3

Cohen, J. D., McClure, S. M., and Yu, A. J. (2007). Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**(1481):933–942. II, 5.4.1

Colella, V., Klopfer, E., and Resnick, M. (2001). Adventures in Modeling: Exploring Complex, Dynamic Systems with StarLogo. Teachers College Press, London. E

Collar, N. (1997). Family Psittacidae (Parrots). In del Hoyo, J., Elliott, A., and Sargatal, J., editors, *Handbook of the Birds of the World: Sandgrouse to Cuckoos*. Lynx Editions, Barcelona. I, 2.3.2, 2.4.3, 3.2.1, 3.4.3, 3.4.3, II, III, 6.2.1, C.1, C.2

Collis, K. and Borgia, G. (2010). The Costs of Male Display and Delayed Plumage Maturation in the Satin Bowerbird (*Ptilonorhynchus violaceus*). *Ethology*, **94**(1):59–71. III

Cook, C., Goodman, N. D., and Schulz, L. E. (2011). Where science starts: Spontaneous experiments in preschoolers exploratory play. *Cognition*, **120**(3):341–349. 6.4.3

Cook, R. G. (2000). The Comparative Psychology of Avian Visual Cognition. *Current Directions in Psychological Science*, **9**(3):83–89. 6.4.1

Cook, R. G., Qadri, M. A. J., Kieres, A., and Commons-Miller, N. (2012). Shape from shading in pigeons. *Cognition*, **124**(3):284–303. 6.4.1

Corballis, M. C. (1983). *Human laterality*. Academic Press, New York. 4.4.2

Cretu, A.-M., Payeur, P., and Petriu, E. M. (2012). Soft object deformation monitoring and learning for model-based robotic hand manipulation. *IEEE Transactions on Systems, Man, and Cybernetics, Part B: Cybernetics*, **42**(3):740–753. 6.4.5

Crevecoeur, F., Giard, T., thonnard, J. L., and Lefevre, P. (2011). Adaptive control of grip force to compensate for static and dynamic torques during object manipulation. *Journal of Neurophysiology*, **106**(6):2973–2981. III, 6.4.4

Cronin, T. W., Kinloch, M. R., and Olsen, G. H. (2005). Head-bobbing behavior in foraging whooping cranes favors visual fixation. *Current Biology*, **15**(7):R243–R244. 2.4.3, 3.2.3, 3.4.2, 4.2.4

Crouzet, S. M. and Serre, T. (2011). What are the visual features underlying rapid object recognition? *Frontiers in Psychology*, **2**:326. III, 6.4.5

Crow, T. J., Crow, L. R., Done, D. J., and Leask, S. (1998). Relative hand skill predicts academic ability: global deficits at the point of hemispheric indecision. *Neuropsychologia*, **36**(12):1275–1282. 3.4.3

Csibra, G. and Gergely, G. (2007). 'Obsessed with goals': functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica*, **124**(1):60–78. 7.4.2

Cunningham, S. J., Alley, M. R., Castro, I., Potter, M. A., Cunningham, M., and Pyne, M. J. (2010). Bill morphology of ibises suggests a remote-tactile sensory system for prey detection. *Auk*, **127**(2):308–316. I, 2.2.3, 2.3.2, 2.4.2, 4.4.2

Cunningham, S. J., Castro, I., and Alley, M. R. (2007). A new prey-detection mechanism for kiwi (*Apteryx* spp.) suggests convergent evolution between paleognathous and neognathous birds. *Journal of Anatomy*, **211**(4):493–502. I, 2.2.3, 2.3.2, 2.4.2, 4.4.2

D

Dall, S., Gosling, S. D., Brown, G. D., and Dingemanse, N. (2012). Variation in Decision Making. In Hammerstein, P. and Stevens, J. R., editors, *Evolution and the Mechanisms of Decision Making*, pages 242–272. MIT Press, Cambridge, MA. II

Dall, S. R. X. and Johnstone, R. A. (2002). Managing uncertainty: information and insurance under the risk of starvation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **357**(1427):1519–1526. II

Dall, S. R. X., McNamara, J. M., and Cuthill, I. C. (1999). Interruptions to foraging and learning in a changing environment. *Animal Behaviour*, **57**(1):9–9. II

Das Gupta, P. and Bryant, P. E. (1989). Young children's causal inferences. *Child Development*, **60**(5):1138–1146. 6.4.6, 7.4.3

Davenport, R. K., Rogers, C. M., and Russell, I. S. (1975). Cross-modal perception in apes: Altered visual cues and delay. *Neuropsychologia*, **13**(2):229–235. III

Davidson, N. S. and Gelman, S. A. (2004). Inductions from novel categories: The role of language and conceptual structure. *Cognitive Development*, **5**(2):151–176. 6.4.6

Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., and Dolan, R. J. (2006). Cortical substrates for exploratory decisions in humans. *Nature*, **441**(7095):876–879. II, 8

de Lorge, J. and Bolles, R. C. (1961). Effects of food deprivation on exploratory behavior in a novel situation. *Perceptual and Motor Skills*, **9**(3):599–606. 5.4.1

de Waal, F. B. M. and Ferrari, P. F. (2010). Towards a bottom-up perspective on animal and human cognition. *Trends in Cognitive Sciences*, **14**(5):201–207. 7.4.5

Demery, Z. P., Arriola-Rios, V. E., Sloman, A., Wyatt, J., and Chappell, J. (2010). Construct to understand: learning through exploration. In *Proceedings of the International Symposium on AI-Inspired Biology*, pages 59–61. 2.4.2, 3.4.3, 5.4.5, III, III, 6.4.4, 6.4.5, 6.4.6, 6.4.6, 6.4.6, 7.4.4, 7.4.5, 7.4.6, 8, E.1

Demery, Z. P., Chappell, J., and Martin, G. R. (2011). Vision, touch and object manipulation in Senegal parrots *Poicephalus senegalus*. *Proceedings of the Royal Society of London B: Biological Sciences*, **278**(1725):3687–3693. I, 2.4.3, 3.1.1, 3.2.3, 3.2.4, 3.4, 3.4.1, 3.4.2, 3.4.3, 3.4.3, 3.4.3, 3.4.3, 4.2.4, 4.2.4, 4.2.2, 4.4.1, 4.4.2, 4.4.3, 4.4.3, II, III

Detry, R., Baseski, E., Popovic, M., Touati, Y., Kruger, N., Kroemer, O., Peters, J., and Piater, J. (2010). Learning continuous grasp affordances by sensorimotor exploration. In Sigaud, O. and Peters, J., editors, *Studies in Computational Intelligence: From Motor Learning to Interaction Learning in Robots*, pages 451–465. Springer, Berlin. 3.4.3

Diamond, A. and Bond, A. B. (1999). *Kea, bird of paradox: the evolution and behavior of a New Zealand parrot*. University of California Press, California. 3.4.3, 4.4.2, III, C.1, C.2

Dickinson, A. (2012). Associative learning and animal cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1603):2733–2742. 1

Dittrich, W., Lea, S., Barrett, J., and Gurr, P. (1998). Categorization of natural movements by pigeons: visual concept discrimination and biological motion. *Journal of the Experimental Analysis of Behavior*, **70**(3):281–299. 7.4.2

Dutant, J., Justo, D., and Pedrini, P. (2004). Motivational aspects of explanatory understanding in humans and apes. In Casati, R., editor, *CNRS School on Object Reference*. 6.4.4

E

Ehrlich, D. (1981). Regional specialization of the chick retina as revealed by the size and density of neurons in the ganglion cell layer. *Journal of Comparative Neurology*, **195**(4):643–657. 2.4.3

Eliassen, S., Jørgensen, C., Mangel, M., and Giske, J. (2007). Exploration or exploitation: life expectancy changes the value of learning in foraging strategies. *Oikos*, **116**(3):513–523. II

Elner, R. and Hughes, R. N. (1978). Energy maximization in the diet of the shore crab, Carcinus maenas. *Journal of Animal Ecology*, **47**(1):103–116. 3.4.3

Engellenner, W. J., Goodlett, C. R., Burright, R. G., and Donovick, P. J. (1982). Environmental enrichment and restriction: effects on reactivity, exploration and maze learning in mice with septal lesions. *Physiology and Behaviour*, **29**(5):885–893. II

Erichsen, J. T. J., Hodos, W. W., Evinger, C. C., Bessette, B. B. B., and Phillips, S. J. S. (1989). Head orientation in pigeons: postural, locomotor and visual determinants. *Brain, Behavior and Evolution*, **33**(5):268–278. 2.4.3

Evans, M. (2001). Environmental enrichment for pet parrots. *In Practice*, **23**(10):596–605. II, 5.4.4

F

Fagen, R. (1985). *Animal play behavior*. Oxford University Press, New York. I

Fehrer, E. (1951). Latent learning in the sophisticated rat. *Journal of Experimental Psychology*, **42**(6):409–416. 2.4.3

Fernandez-Juricic, E., O'Rourke, C., and Pitlik, T. (2010). Visual coverage and scanning behavior in two corvid species: American crow and Western scrub jay. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology*, **196**(12):879–888. 3.4.3

Ferreira, R. G., Emidio, R. A., and Jerusalinsky, L. (2010). Three stones for three seeds: natural occurrence of selective tool use by capuchins (*Cebus libidinosus*) based on an analysis of the weight of stones found at nutting sites. *American Journal of Primatology*, **72**(3):270–275. 4.4.2, 6.4.3

Ficken, M. S. (1977). Avian play. *Auk*, **94**:573–582. I, 2.4.2, III

Floreano, D. and Mattiussi, C. (2008). *Bio-Inspired Artificial Intelligence: Theories, Methods, and Technologies*. MIT Press, Cambridge, MA. 3.4.3

Fodor, J. A. (1983). *The Modularity of Mind : an essay on faculty psychology*. MIT Press, Cambridge, MA. 7.4.4

Forsaw, J. M. (1977). *Parrots of the World*. T. F. H. Publications, Neptune. 2.4.3

Forster, F. C. (1995). Exploratory behavior and learning in laboratory marmosets (*Callithrix jacchus jacchus*): Comparisons between experimental-cage and home-cage activity. *Primates*, **36**(4):501–514. II

Fox, R. A. and Millam, J. R. (2004). The effect of early environment on neophobia in orange-winged Amazon parrots (*Amazona amazonica*). *Applied Animal Behaviour Science*, **89**(1-2):117–129. 5.4.1, 8

Frey, J. R. and Kaiser, A. P. (2011). The Use of Play Expansions to Increase the Diversity and Complexity of Object Play in Young Children With Disabilities. *Topics in Early Childhood Special Education*, **31**(2):99–111. 6.4.2

Friedmann, H. and Davis, M. (1938). "Left-handedness" in parrots. *Auk*, **55**(3):478–480. 2.4.1, 2.4.2, 2.4.3, 3.4.3, 3.4.3

Funk, M. S. (1996a). Development of object permanence in the New Zealand parakeet (*Cyanoramphus auriceps*). *Learning and Behavior*, **24**(4):375–383. 6.2.1, 6.2.4, 6.2.2

Funk, M. S. (1996b). Spatial skill development in golden-crowned parakeets (*Cyanoramphus auriceps*): a Piagetian assessment. *Bird Behaviour*, **11**(2):91–104. 6.2.1, 6.2.4, 6.2.2

Funk, M. S. (2002). Problem solving skills in young yellow-crowned parakeets (*Cyanoramphus auriceps*). *Animal Cognition*, **5**(3):167–176. III, III, 6.2.1, 6.2.4, 6.2.2, 8

Funk, M. S. and Matteson, R. L. (2004). Stable individual differences on developmental tasks in young yellow-crowned parakeets, *Cyanoramphus auriceps*. *Learning and Behavior*, **32**(4):427–439. 3.4.3, II, 6.2.1, 6.2.4, 6.2.2

Fuszara, M., Jablonski, P. G., Lee, S.-i., and Fuszara, E. (2012). Working hard for peanuts: Mexican jays Aphelocoma ultramarina assessing their food. In *ASAB Interdisciplinary Workshop 2012: Physical Cognition & Problem Solving*. 6.4.3

G

Gajdon, G. K., Amann, L., and Huber, L. (2011). Keas rely on social information in a tool use task but abandon it in favour of overt exploration. *Interaction Studies*, **12**(2):304–323. III

Gajdon, G. K., Fijn, N., and Huber, L. (2006). Limited spread of innovation in a wild parrot, the kea (Nestor notabilis). *Animal Cognition*, **9**:173–181. 3.4.3

Gamble, J. R. and Cristol, D. A. (2002). Drop-catch behaviour is play in herring gulls, *Larus argentatus*. *Animal Behaviour*, **63**(2):339–345. III

Gardner, E. B., Boitano, J., Mancino, N. S., and D'Amico, D. P. (1975). Environmental enrichment and deprivation: effects on learning, memory and exploration. *Physiology and Behaviour*, **14**(3):321–327. II

Garner, J. P., Meehan, C. L., Famula, T. R., and Mench, J. A. (2006). Genetic, environmental, and neighbor effects on the severity of stereotypies and feather picking in Orange-winged Amazon parrots (*Amazona amazonica*): an epidemiological study. *Applied Animal Behaviour Science*, **96**(1-2):153–168. II, 5.4.4

Garner, J. P., Meehan, C. L., and Mench, J. A. (2003). Stereotypies in caged parrots, schizophrenia and autism: evidence for a common mechanism. *Behavioural Brain Research*, **145**(1-2):125–134. II, 5.4.4

Gaver, W. (1996). Affordances for interaction: The social is material for design. *Ecological Psychology*, **8**(2):111–129. 6.4.6

Genaro, G. and Schmidek, W. (2000). Exploratory activity of rats in three different environments. *Ethology*, **106**(9):849–859. II

Gentle, M. J. and Breward, J. (1986). The bill tip organ of the chicken (*Gallus gallus* var. *domesticus*). *Journal of Anatomy*, **145**:79–85. I, 2.2.3, 2.3.2, 4.4.2

Gentsch, C. C., Lichtsteiner, M. M., and Feer, H. H. (1982). Behavioural comparisons between individually- and group-housed male rats: effects of novel environments and diurnal rhythm. *Behavioural Brain Research*, **6**(1):93–100. 5.4.1

Gerstadt, C. L., Hong, Y. J., and Diamond, A. (1994). The relationship between cognition and action: performance of children 3 1/2-7 years old on a Stroop-like day-night test. *Cognition*, **53**(2):129–153. 7.4.2

Gibson, E. J. (1988). Exploratory behavior in the development of perceiving, acting, and the acquiring of knowledge. *Annual Reviews of Psychology*, **39**(1):1–42. 1, I, 2.4.2, 5.4.1, III, III, 6.4.5, 6.4.6

Gibson, E. J. and Pick, A. (2003). *An Ecological Approach to Perceptual Learning and Development*. Oxford University Press, New York. 6.4.6

Gibson, E. J., Riccio, G. E., Schmuckler, M. A., Stoffregen, T. A., Rosenbaum, D. A., and Taormina, J. (1987). Detection of the traversability of surfaces by crawling and walking infants. *Journal of Experimental Psychology: Human Perception and Performance*, **13**(4):533–544. 6.4.5

Gibson, E. J. and Walker, A. S. (1984). Development of knowledge of visual-tactual affordances of substance development of knowledge of visual-tactual affordances of substance. *Child Development*, **55**(2):453–460. 3.4.3, 4.4.2, 6.4.5, 6.4.6

Gibson, J. J. (1950). *The perception of the visual world*. Houghton Miffin, Boston. 6.4.1

Gibson, J. J. (1958). Visually controlled locomotion and visual orientation in animals. *British Journal of Psychology*, **49**(906464858):182–194. 2.4.3

Gibson, J. J. (1962). Observations on active touch. *Psychological Review*, **69**:477–491. 1, 3.4.3, 6.4.6

Gibson, J. J. (1977). The theory of affordances. In Shaw, R. and Bransford, J., editors, *Perceiving, acting, and knowing: Toward an ecological psychology*, pages 67–82. Erlbaum, Hillsdale, NJ. III

Glickman, S. E. and Sroges, R. W. (1966). Curiosity in zoo animals. *Behaviour*, **26**(1):151–188. 1, III

Glymour, C. N. (2003). Learning, prediction and causal Bayes nets. *Trends in Cognitive Sciences*, **7**(1):43–48. 1, 6.4.6

Goodale, M. A. (1983). Visually guided pecking in the pigeon (*Columba livia*). *Brain, Behavior and Evolution*, **22**(1):22–41. 2.4.3

Goodnow, J. J. (1969). Effects of active handling, illustrated by uses for objects. *Child Development*, **40**(1):201–212. 6.4.6

Gopnik, A. (1996). The Scientist as Child. *Philosophy of Science*, **63**(4):485–514. 6.4.6

Gopnik, A. (2000). Explanation as orgasm and the drive for causal understanding: the evolution, function and phenomenology of the theory-formation system. In Keil, F. C. and Wilson, R. A., editors, *Explanation and cognition*, pages 299–323. The MIT Press, Cambridge, MA. 1, 6.4.4

Gopnik, A., Glymour, C. N., Sobel, D. M., Schulz, L. E., Kushnir, T., and Danks, D. (2004). A theory of causal learning in children: causal maps and Bayes nets. *Psychological Review*, **111**(1):3–32. 6.4.6

Gopnik, A. and Meltzoff, A. N. (1998). *Words, Thoughts, and Theories*. MIT Press. 6.4.6

Gopnik, A. and Schulz, L. E. (2004). Mechanisms of theory formation in young children. *Trends in Cognitive Sciences*, **8**(8):371–377. 1

Gopnik, A. and Schulz, L. E. (2007). *Causal Learning: Psychology, Philosophy, And Computation*. Oxford University Press, London. 6.4.6

Gopnik, A. and Wellman, H. M. H. (2012). Reconstructing constructivism: Causal models, Bayesian learning mechanisms, and the theory theory. *Psychological Bulletin*, **138**(6):1085–1108. 6.4.6

Gortz, N., Lewejohann, L. L., Tomm, M. M., Ambrée, O. O., Keyvani, K. K., Paulus, W., and Sachser, N. (2008). Effects of environmental enrichment on exploration, anxiety, and memory in female TgCRND8 Alzheimer mice. *Behavioural Brain Research*, **191**(1):43–48. II

Gottschaldt, K. M. and Lausmann, S. (1974). The peripheral morphological basis of tactile sensibility in the beak of geese. *Cell and Tissue Research*, **153**(4):477–496. I, 2.2.3, 2.3.2, 4.4.2

Goujon, D. E. (1869). Sur un appareil de corpuscules tactiles situe dans le bec des perroquets. *Journal de l'Anatomie et de la Physiologie Normales et Pathologiques de l'Homme*, **6**:449–455. I, 2.2.3, 2.3.2, 2.4.3, 3.4.3, 4.4.2

Gould, J. P. (1974). Risk, stochastic preference, and the value of information: A comment. *Journal of Economic Theory*, **8**:64–84. 1, II

Grant, R. A., Mitchinson, B., Fox, C. W., and Prescott, T. J. (2009). Active touch sensing in the rat: anticipatory and regulatory control of whisker movements during surface exploration. *Journal of Neurophysiology*, **101**(2):862–874. 3.4.3, III, 6.4.4

Grasso, F. W. and Basil, J. A. (2009). The evolution of flexible behavioral repertoires in cephalopod molluscs. *Brain, Behavior and Evolution*, **74**(3):231–245. 1, 3.4.3, II

Green, P. R. (1998). Head orientation and trajectory of locomotion during jumping and walking in domestic chicks. *Brain, Behavior and Evolution*, **51**(1):48–58. 2.4.3, 3.2.3, 3.4.1

Green, P. R., Davies, M. N., and Thorpe, P. H. (1992). Head orientation in pigeons during landing flight. *Vision Research*, **32**(12):2229–2234. 2.4.3

Greenberg, R. (1983). The role of neophobia in determining the degree of foraging specialization in some migrant warblers. *American Naturalist*, **122**(4):444–453. 6.4.2

Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In Reader, S. M. and Laland, K. N., editors, *Animal Innovation*, pages 175–196. Oxford University Press, New York. II

Greenberg, R. and Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia in birds. **16**:119–178. 1, II, 5.4.3

Greene, T. C. (1988). *Behavioural Ecology of the Red-crowned Parakeet (*Cyanoramphus novaezelandiae *Sparrman, 1787) and the Yellow-crowned Parakeet (*Cyanoramphus auriceps *Kuhl, 1820) on Little Barrier Island*. PhD thesis, University of Auckland, London. 3.4.3, II, 6.2.1, C.2

Greene, T. C. (1998). Foraging ecology of the red-crowned parakeet (*Cyanoramphus novaezelandiae novaezelandiae*) and yellow-crowned parakeet (*C. auriceps auriceps*) on Little Barrier Island, Hauraki Gulf, New Zealand. *New Zealand Journal of Ecology*, **22**(2):161–171. 3.4.3, 4.4.2, II, 5.4.1, III, 6.2.1

Grønhaug, H. (2006). *Foraging ecology and learning: adaptive behavioural strategies and the value of information*. PhD thesis. II

Guillemain, M., Martin, G. R., and Fritz, H. (2002). Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Functional Ecology*, **16**(4):522–529. I

Gunderson, V. M., Rose, S. A., and Grant-Webster, K. S. (1990). Cross-moda transfer in high- and low-risk infant pigtailed macaque monkeys. *Developmental Psychology*, **26**(5):576–581. III

Gutierrez-Ibanez, C., Iwaniuk, A. N., and Wylie, D. R. W. (2009). The independent evolution of the enlargement of the principal sensory nucleus of the trigeminal nerve in three different groups of birds. *Brain, Behavior and Evolution*, **74**(4):280–294. I, 3.4.3, 4.4.2

H

Hall, S. L. (1998). Object play by adult animals. In Bekoff, M. and Byers, J. A., editors, *Animal Play: Comparative, and Ecological Perspectives*, pages 45–60. Cambridge University Press, Cambridge. 6.2.1

Hall, S. L. and Bradshaw, J. W. S. (1998). The influence of hunger on object play by adult domestic cats. *Applied Animal Behaviour Science*, **58**(1):143–150. III

Hamner, P. and Hamner, W. M. (1977). Chemosensory tracking of scent trails by the planktonic shrimp *Acetes sibogae australis*. *Science*, **195**:886–888. 3.4.3

Hansell, M. and Ruxton, G. D. (2008). Setting tool use within the context of animal construction behaviour. *Trends in Ecology and Evolution*, **23**(2):73–78. III

Hanus, D. and Call, J. (2008). Chimpanzees infer the location of a reward on the basis of the effect of its weight. *Current Biology*, **18**(9):R370–R372. 6.4.3

Hanus, D. and Call, J. (2011). Chimpanzee problem-solving: contrasting the use of causal and arbitrary cues. *Animal Cognition*, **14**(6):871–878. 6.4.3

Harlow, H. F., Harlow, M., and Meyer, D. R. (1950). Learning motivated by a manipulation drive. *Journal of Experimental Psychology*, **40**(2):228–234. 1, II, III, 6.4.2, 6.4.6

Harris, L. J. (1989). Footedness in parrots: three centuries of research, theory, and mere surmise. *Canadian Journal of Psychology*, **43**(3):369–396. 2.4.1, 2.4.2, 2.4.3, 3.4.3, 3.4.3, 3.4.3, 4.4.3

Hart, N., Partridge, J., and Cuthill, I. C. (2000). Retinal asymmetry in birds. *Current Biology*, **10**(2):115–117. 4.4.3

Haruno, M., Wolpert, D. M., and Kawato, M. (2001). Mosaic model for sensorimotor learning and control. *Neural Computation*, **13**(10):2201–2220. 3.4.3

Haselgrove, M. (2010). Reasoning rats or associative animals? A common-element analysis of the effects of additive and subadditive pretraining on blocking. *Journal of Experimental Psychology: Animal Behavior Processes*, **36**(2):296–306. 1

Hassan, E. S. (1989). Hydrodynamic imaging of the surroundings by the lateral line of the blind cave fish *Anoptichthys jordani*. pages 217–228. Springer-Verlag, New York. 3.4.3

Haun, D. B. M., Jordan, F. M., Vallortigara, G., and Clayton, N. S. (2010). Origins of spatial, temporal and numerical cognition: Insights from comparative psychology. *Trends in Cognitive Sciences*, **14**(12):552–560. 5.4.1

Hawes, N., Hanheide, M., Sjoo, K., Aydemir, A., Jensfelt, P., Gobelbecker, M., Brenner, M., Zender, H., Lison, P., Kruijff-Korbayova, I., Kruijff, G. J. M., and Zillich, M. (2010). Dora the Explorer: a motivated robot. In *Proceedings of the 9th International Conference on Autonomous Agents and Multiagent Systems*, pages 1617–1618. International Foundation for Autonomous Agents and Multiagent Systems. 1

Hawkins, P., Morton, D. B., Cameron, D., Cuthill, I. C., Francis, R., Freire, R., Gosler, A., Healy, S. D., Hudson, A., Inglis, I. R., Kirkwood, J., Lawton, M., Monaghan, P., Sherwin, C., and Townsend, P. (2001). Laboratory birds: refinements in husbandry and procedures. *Laboratory Animals*, **35**(Supplement 1):103–112. 2.4.3, 4.2.1, 5.2.2, 5.4.4, 6.2.1

Hayashi, M. and Takeshita, H. (2006). Cognitive development in apes and humans assessed by object manipulation. In Matsuzawa, T. and Tanaka, M., editors, *Cognitive Development in Chimpanzees*. Spinger, Berlin. III, C.1

Heinrich, B. (1995). Neophilia and exploration in juvenile common ravens, *Corvus corax*. *Animal Behaviour*, **50**(3):695–704. II, 5.4.3, III

Henderson, B. (1988). Individual differences in exploration: A replication and extension. *Journal of Genetic Psychology*, **149**(4):555–557. 6.4.6

Henderson, B. and Moore, S. G. (1980). Children's responses to objects differing in novelty in relation to level of curiosity and adult behavior. *Child Development*, **51**(2):457–465. 6.4.3, 6.4.6, 6.4.6

Hengstenberg, R. (1988). Mechanosensory control of compensatory head roll during flight in the blowfly *Calliphora erythrocephala* Meig. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology*, **163**(2):151–165. 2.4.3

Hennessy, M. B., Smotherman, W. P., and Levine, S. (1977). Early olfactory enrichment enhances later consumption of novel substances. *Physiology and Behaviour*, **19**(4):481–483. II

Heppner, F. H. and Anderson, J. (1985). Leg thrust important in flight take-off in the pigeon. *Journal of Experimental Biology*, **114**(1):285–288. 2.4.3, 3.4

Heyes, C. (2011). What's social about social learning? *Journal of Comparative Psychology*, **126**(2):193–202. 1

Heyser, C. J. and Chemero, A. (2012). Novel object exploration in mice: not all objects are created equal. *Behavioural Processes*, **89**(3):232–238. III, III, 6.4.3

Hirsh-Pasek, K. (2008). Why play= learning. In *Encyclopedia on Early Childhood Development*. Centre of Excellence for Early Childhood Development, London. III

Hodos, W. W. and Erichsen, J. T. J. (1990). Lower-field myopia in birds: an adaptation that keeps the ground in focus. *Vision Research*, **30**(5):653–657. 2.4.3, 2.4.3

Homberger, D. G. (1980). *Functional morphology and evolution of the feeding apparatus in parrots, with special reference to the Pesquet's Parrot, Psittrichas fulgidus (Lesson)*. Conservation of new world parrots (Pasquier RF, London. I, 3.4.3

Homberger, D. G. (2003). The comparative biomechanics of a prey–predator relationship: the adaptive morphologies of the feeding apparatus of Australian black-cockatoos and their foods as a basis for the reconstruction of the evolutionary history of the Psittaciformes. In Bels, V., Casinos, A., and Gasc, J. P., editors, *Vertebrate Biomechanics and Evolution*, pages 203–228. BioS Scientific Publishers, Oxford. I

Hood, B. M. (1995). Gravity rules for 2-to 4-year olds? *Cognitive Development*, **10**(4):577–598. 6.4.3

Hood, B. M., Carey, S. E., and Prasada, S. (2000). Predicting the outcomes of physical events: two-year-olds fail to reveal knowledge of solidity and support. *Child Development*, **71**(6):1540–1554. 7.4.1, 7.4.2

Hood, B. M., Wilson, A., and Dyson, S. (2006). The effect of divided attention on inhibiting the gravity error. *Developmental Science*, **9**(3):303–308. 6.4.6, 7.4.2

Houpt, K., Houpt, T. R., Johnson, J. L., Erb, H. N., and Yeon, S. C. (2001). The effect of exercise deprivation on the behaviour and physiology of straight stall confined pregnant mares. *Animal Welfare*, **10**(3):257–267. 5.4.1

Houston, A. I., Krebs, J. R., and Erichsen, J. T. (1980). Optimal prey choice and discrimination time in the great tit (*Parus major L.*). *Behavioral Ecology and Sociobiology*, **6**(3):169–175. II

Huang, F. L., Huang, K.-P., and Boucheron, C. (2007). Long-term enrichment enhances the cognitive behavior of the aging neurogranin null mice without affecting their hippocampal LTP. *Learning and Memory*, **14**(8):512–519. II

Huber, L. and Gajdon, G. K. (2006). Technical intelligence in animals: the kea model. *Animal Cognition*, **9**(4):295–305. I, 3.4.3, II, 7.4.5

Huber, L., Rechberger, S., and Taborsky, M. (2001). Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Animal Behaviour*, **62**(5):945–954. 1

Hughes, A. (1977). The topography of vision in mammals of contrasting life style: comparative optics and retinal organisation. In Crecitelli, F., editor, *Handbook fo Sensory Physiology*, pages 613–756. Springer-Verlag, Berlin. I, 2.4.3

Hughes, B. O. and Duncan, I. J. H. (1988). The notion of ethological 'need', models of motivation and animal welfare. *Animal Behaviour*, **36**(6):1696–1707. 5.4.1

Hughes, R. N. (1997). Intrinsic exploration in animals: motives and measurement. *Behavioural Processes*, **41**(3):213–226. II, 5.4.1, 5.4.3

Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, **379**(6562):249–251. III

Hunt, G. R. (2000). Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proceedings of the Royal Society of London B: Biological Sciences*, **267**(1441):403–413. III

Hunt, G. R., Corballis, M. C., and Gray, R. D. (2001). Animal behaviour: laterality in tool manufacture by crows. *Nature*, **414**(6865):707. 3.4.3, 4.4.3

Hunt, J. M. (1965). Intrinsic motivation and its role in psychological development. In Levine, D., editor, *Nebraska symposium on motivation*, pages 189–282. University of Nebraska Press, Lincoln. 6.4.6

I

Inglis, I. R. (1983). Towards a cognitive theory of exploratory behaviour . In Archer, J. and Birke, L. I. A., editors, *Exploration in Animals and Humans: comparative psychology of animals and humans*, pages 72–117. Van Nostrand Reinhold, Workingham. 1, III, 6.4.5, 7.4.3

Inglis, I. R. (2000). Review: The central role of uncertainty reduction in determining behaviour. *Behaviour*, **137**(12):1567–1599. II

Inglis, I. R. and Langton, S. (2006). How an animal's behavioural repertoire changes in response to a changing environment: a stochastic model. *Behaviour*, **143**:1563–1596. 1, 5.4.3

Inglis, I. R., Langton, S., Forkman, B., and Lazarus, J. (2001). An information primacy model of exploratory and foraging behaviour. *Animal Behaviour*, **62**(3):543–557. II, 6.4.3

Inglis, I. R. and Shepherd, D. S. (2010). Rats work for food they then reject: support for the information-primacy approach to learned industriousness. *Ethology*, **98**(2):154–164. III

Isler, K. (2003). Gait parameters in vertical climbing of captive, rehabilitant and wild Sumatran orang-utans (*Pongo pygmaeus abelii*). *Journal of Experimental Biology*, **206**(22):4081–4096. 2.4.3, 3.4

Iwaniuk, A. N., Dean, K. M., and Nelson, J. E. (2005). Interspecific allometry of the brain and brain regions in parrots (Psittaciformes): comparisons with other birds and primates. *Brain, Behavior and Evolution*, **65**(1):40–59. I

J

James, W. (1890). *The principles of psychology*. H. Holt and company. 6.4.6

Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science*, **219**(4581):187–189. II

Jarvis, E. D., Gunturkun, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D. J., Shimizu, T., Striedter, G. F., Wild, J. M., Ball, G. F., Dugas-Ford, J., Durand, S. E., Hough, G. E., Husband, S., Kubikova, L., Lee, D. W., Mello, C. V., Powers, A., Siang, C., Smulders, T. V., Wada, K., White, S., Yamamoto, K., Yu, J., Reiner, A., Butler, A. B., and Avian Brain Nomenclature Consortium (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience*, **6**(2):151–159. I

Jennings, K. D., Harmon, R. J., Morgan, G. A., Gaiter, J. L., and Yarrow, L. J. (1979). Exploratory play as an index of mastery motivation: Relationships to persistence, cognitive functioning, and environmental measures. *Developmental Psychology*, **15**(4):386–394. 5.4.1

Jones, R. B., Larkins, C., and Hughes, B. O. (1996). Approach/avoidance responses of domestic chicks to familiar and unfamiliar video images of biologically neutral stimuli. *Applied Animal Behaviour Science*, **48**(1):81–98. 6.4.2

K

Kacelnik, A. and Krebs, J. R. (1985). Learning to exploit patchily distributed food. In Sibly, R. M. and Smith, R. H., editors, *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*, pages 189–205. Blackwell Scientific Publications, Oxford. II

Kaelbling, L. P., Littman, M. L., and Cassandra, A. R. (1998). Planning and acting in partially observable stochastic domains. *Artificial Intelligence*, **101**(1-2):99–134. II

Kalmar, I. D., Janssens, G. P. J., and Moons, C. P. H. (2010). Guidelines and ethical considerations for housing and management of psittacine birds used in research. *ILAR Journal*, **51**(4):409–423. 4.2.1, 5.2.2, 5.4.4, 6.2.1

Kalmar, I. D., Moons, C. P. H., Meers, L. L., and Janssens, G. P. J. (2007). Psittacine birds as laboratory animals: refinements and assessment of welfare. *Journal of the American Association for Laboratory Animal Science*, **46**(4):8–15. 4.2.1, 5.2.2, 5.4.4, 6.2.1

Kampmer, N. L., Cornwell, K. S., Fitzgerald, H. E., and Harris, L. J. (1985). Motor asymmetries in the human infant: stepping movements. *Infant Mental Health Journal*, **6**:145–157. 3.4.3

Karmiloff-Smith, A. (1995). *Beyond Modularity: A Developmental Perspective on Cognitive Science*. MIT Press, London, 4 edition. 1, III, 6.4.5, 6.4.6, 6.4.6, 7.4.2, 7.4.4

Karmiloff-Smith, A. and Inhelder, B. (1975). If you want to get ahead, get a theory. *Cognition*, **3**(3):195–212. 1

Kawa, R. and Pisula, E. (2010). Locomotor activity, object exploration and space preference in children with autism and Down syndrome. *Acta Neurobiologiae Experimentalis*, **70**(2):131–140. 6.4.2

Kearvell, J. C., Young, J. R., and Grant, A. D. (2002). Comparative ecology of sympatric orange-fronted parakeets (*Cyanoramphus malherbi*) and yellow-crowned parakeets (*C. auriceps*), South Island, New Zealand. *New Zealand Journal of Ecology*, **26**(2):139–148. 3.4.3, II, III, 6.2.1, C.2

Keary, N. and Bischof, H.-J. (2012). Activation changes in zebra finch (Taeniopygia guttata) brain areas evoked by alterations of the earth magnetic field. *PloS One*, **7**(6):e38697. 3.4.3

Kijne, M. and Kotrschal, K. (2002). Neophobia affects choice of food-item size in group-foraging common ravens (*Corvus corax*). *Acta Ethologica*, **5**(1):13–18. III

Kim, L. C., Garner, J. P., and Millam, J. R. (2009). Preferences of Orange-winged Amazon parrots (*Amazona amazonica*) for cage enrichment devices. *Applied Animal Behaviour Science*, **120**(3-4):216–223. II, 5.4.3

King, A. S. and McLelland, J. (1979). *Form and Function in Birds*. Academic Press, New York. I

Kjaersgaard, A., Pertoldi, C., Loeschcke, V., and Witzner Hansen, D. (2008). Tracking the gaze of birds. *Journal of Avian Biology*, **39**(4):466–469. 2.4.3, 4.4.1, 8

Klatzky, R. L. and Lederman, S. J. (1993). Toward a computational model of constraint-driven exploration and haptic object identification. *Perception*, **22**(5):597–621. 6.4.2, 6.4.5

Klatzky, R. L., Lederman, S. J., and Matula, D. E. D. (1991). Imagined haptic exploration in judgments of object properties. *Journal of Experimental Psychology: Learning, Memory and Cognition*, **17**(2):314–322. 6.4.2

Koehler, D. J. and James, G. (2009). Probability matching in choice under uncertainty: Intuition versus deliberation. *Cognition*, **113**(1):123–127. II, 5.4.3

Kraft, D., Detry, R., Pugeault, N., Baseski, E., Guerin, F., Piater, J. H., and Kruger, N. (2010). Development of object and grasping knowledge by robot exploration. In *IEEE Transactions on Autonomous Mental Development*, pages 368–383. 3.4.3

Krechevsky, I. (1932). "Hypotheses" in rats. *Psychological Review*, **39**(6):516–532. 1

Kuba, M. J., Byrne, R. A., Meisel, D. V., and Mather, J. A. (2006a). Exploration and habituation in intact free moving *Octopus vulgaris*. *International Journal of Comparative Psychology*, **19**(4):426–438. 3.4.3, II

Kuba, M. J., Byrne, R. M. J., Meisel, D. V., and Mather, J. A. (2006b). When do octopuses play? Effects of repeated testing, object type, age, and food deprivation on object play in *Octopus vulgaris*. *Journal of Comparative Psychology*, **120**(3):184–190. III

Kuba, M. J., Meisel, D. V., Byrne, R. A., Griebel, U., and Mather, J. A. (2003). Looking at play in Octopus vulgaris. *Berliner Palaobiol. Abh.*, **3**:163–169. III

Kuhn, D. (1989). Children and adults as intuitive scientists. *Psychological Review*, **96**(4):674–689. 6.4.6

Kuhn, D. and Dean Jr, D. (2004). Connecting Scientific Reasoning and Causal Inference. *Journal of Cognition and Development*, **5**(2):261–288. 6.4.6, 6.4.6

Kundey, S. M. A., De Los Reyes, A., Taglang, C., Baruch, A., and German, R. (2010). Domesticated dogs' (*Canis familiaris*) use of the solidity principle. *Animal Cognition*, **13**(3):497–505. 7.4.2

L

Lansink, J. M., Mintz, S., and Richards, J. E. (2000). The distribution of infant attention during object examination. *Developmental Science*, **3**(2):163–170. 6.4.6

Leca, J.-B., Gunst, N., and Huffman, M. A. (2011). Complexity in object manipulation by Japanese macaques (*Macaca fuscata*): a cross-sectional analysis of manual coordination in stone handling patterns. *Journal of Comparative and Physiological Psychology*, **125**(1):61–71. 3.4.3

Lederman, S. J. and Klatzky, R. L. (1987). Hand movements: a window into haptic object recognition. *Cognitive Psychology*, **19**(3):342–368. 6.4.1, 6.4.6

Lederman, S. J. and Klatzky, R. L. (1993). Extracting object properties through haptic exploration. *Acta Psychologica*, **84**(1):29–40. 3.4.3, 6.4.6

Lee, S.-A. and Spelke, E. S. (2011). Young children reorient by computing layout geometry, not by matching images of the environment. *Psychonomic Bulletin and Review*, **18**(1):192–198. 6.4.1

Lee, S.-i., Jeong, C., Lee, W. Y., Fuszara, M., Fuszara, E., Song, S., Brown, J., and Jablonski, P. G. (2012). Weight perception in Mexican jays. In *ASAB Interdisciplinary Workshop 2012: Physical Cognition & Problem Solving*. III, 6.4.3

Lefebvre, L., Reader, S. M., and Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution*, **63**(4):233–246. I, II

Legare, C. H. (2012). Exploring Explanation: Explaining Inconsistent Evidence Informs Exploratory, Hypothesis-Testing Behavior in Young Children. *Child Development*, **83**(1):173–185. 1, 6.4.6

Lockman, J. (2000). A perception–action perspective on tool use development. *Child Development*, **71**(1):137–144. 6.4.1

Loewenstein, G. (1994). The psychology of curiosity: A review and reinterpretation. *Psychological Bulletin*, **116**(1):75–98. 1

Lopes, M. and Oudeyer, P.-Y. (2010). Guest Editorial: Active learning and intrinsically motivated exploration in robots: advances and challenges. In *IEEE Transactions on Autonomous Mental Development*, pages 65–69. 1

Luescher, A. U. (2006). *Manual Of Parrot Behavior*. Blackwell, San Francisco. 1, I, 2.4.1, 2.4.3, 3.4.3, 4.4.1, II, 5.4.1, III, III, 6.2.1, 6.4.5

Lumeij, J. T. and Hommers, C. J. (2008). Foraging 'enrichment' as treatment for pterotillomania. *Applied Animal Behaviour Science*, **111**(1-2):85–94. II, 5.4.4

M

Magat, M. and Brown, C. (2009). Laterality enhances cognition in Australian parrots. *Proceedings of the Royal Society of London B: Biological Sciences*, **276**(1676):4155–4162. 2.4.1, 2.4.2, 2.4.3, 3.4.3, 3.4.3, 3.4.3, 4.4, 4.4.3, 3, 4.4.3

Magrath, R. D. and Lill, A. (1983). The Use of Time and Energy by the Crimson Rosella in a Temperate Wet Forest in Winter. *Australian Journal of Zoology*, **31**(6):903. 5.4.1

Manduell, K. L., Morrogh-Bernard, H. C., and Thorpe, S. K. S. (2011). Locomotor behavior of wild orangutans (*Pongo pygmaeus wurmbii*) in disturbed peat swamp forest, Sabangau, Central Kalimantan, Indonesia. *American Journal of Physical Anthropology*, **145**(3):348–359. 2.4.3, 3.4

Manrique, H. M., Sabbatini, G., Call, J., and Visalberghi, E. (2011). Tool choice on the basis of rigidity in capuchin monkeys. *Animal Cognition*, **14**(6):775–786. 6.4.5

Marsh, H. L. H. and MacDonald, S. E. S. (2012). Orangutans (Pongo abelii) "play the odds": information-seeking strategies in relation to cost, risk, and benefit. *Journal of Comparative Psychology*, **126**(3):263–278. II

Martin, G. R. (1984). The visual fields of the tawny owl, *Strix aluco L.* *Vision Research*, **24**(12):1739–1751. 2.2.2

Martin, G. R. (1986a). The eye of a passeriform bird, the European starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology*, **159**(4):545–557. I

Martin, G. R. (1986b). Total panoramic vision in the mallard duck, *Anas platyrhynchos*. *Vision Research*, **26**(8):1303–1305. I

Martin, G. R. (1994). Visual fields in woodcocks *Scolopax rusticola* (Scolopacidae; Charadriiformes). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology*, **174**(6):787–793. I, 4.4.1

Martin, G. R. (2007). Visual fields and their functions in birds. *Journal of Ornithology*, **148**(S2):547–562. I, 2.2.2, 2.4.1, 2.4.1, 2.4.3, 2.4.3, 3.4.3, 4.2.4, 4.4.1

Martin, G. R. (2009). What is binocular vision for? A birds' eye view. *Journal of Vision*, **9**(11):14–14. I, 2.4.1, 2.4.3, 3.4.2, 3.4.3, 4.4.1

Martin, G. R. (2011). Through birds' eyes: insights into avian sensory ecology. *Journal of Ornithology*, pages 1–26. 2.2.1, 2.3.1, 2.4.3, 3.4.1

Martin, G. R. and Coetzee, H. C. (2004). Visual fields in hornbills: precision-grasping and sunshades. *Ibis*, **146**(1):18–26. 2.4.2

Martin, G. R. and Katzir, G. (1994). Visual fields and eye movements in herons (Ardeidae). *Brain, Behavior and Evolution*, **44**(2):74–85. I

Martin, G. R. and Katzir, G. (1999). Visual fields in Short-Toed Eagles, *Circaetus gallicus* (Accipitridae), and the function of binocularity in birds. *Brain, Behavior and Evolution*, **53**(2):55–66. I, 3.4.2

Martin, G. R. and Shaw, J. M. (2010). Bird collisions with power lines: failing to see the way ahead? *Biological Conservation*, **143**(11):2695–2702. 2.2.2, 3.4.1, 3.4.2

Martin, G. R., White, C. R., and Butler, P. J. (2008). Vision and the foraging technique of Great Cormorants *Phalacrocorax carbo*: pursuit or close-quarter foraging? *Ibis*, **150**(3):485–494. 2.4.2

Martin, G. R., Wilson, K.-J., Wild, J. M., Parsons, S., Fabiana Kubke, M., and Corfield, J. R. (2007). Kiwi forego vision in the guidance of their nocturnal activities. *PloS One*, **2**(2):e198. 2.4.2

Martin, G. R. and Young, S. R. (1983). The retinal binocular field of the pigeon (*Columba livia*: English racing homer). *Vision Research*, **23**(9):911–915. 2.4.3

Mash, C., Keen, R., and Berthier, N. E. (2003). Visual access and attention in two-year-olds' event reasoning and object search. *Infancy*, **4**(3):371–388. 6.4.6

Masnick, A. M. (2002). Reasoning from data: the effect of sample size and variability on children's and adults' conclusions. In *Proceedings of the 24th annual conference of the Cognitive Science Society*, pages 643–648. 6.4.6

Matsuzawa, T. and Tanaka, M. (2006). *Cognitive Development in Chimpanzees*, volume 78. Springer, Berlin. III

McCall, R. B. (2011). Exploratory manipulation and play in the human infant. *Monographs of the Society for Research in Child Development*, **39**(2):1–88. 6.4.6

McReynolds, P., Acker, M., and Pietila, C. (1961). Relation of object curiosity to psychological adjustment in children. *Child Development*, **32**:393–400. 6.4.6, 7.4.4

Meehan, C. L. and Mench, J. A. (2002). Environmental enrichment affects the fear and exploratory responses to novelty of young Amazon parrots. *Applied Animal Behaviour Science*, **79**(1):75–88. II, 5.4.1, 6.4.2

Meehan, C. L. and Mench, J. A. (2007). The challenge of challenge: can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, **102**(3-4):246–261. II, III

Meehan, C. L., Millam, J. R., and Mench, J. A. (2002). Foraging opportunity and increased physical complexity both prevent and reduce psychogenic feather picking by young Amazon parrots . *Applied Animal Behaviour Science*, **80**(1):71–85. II, 6.4.2

Mench, J. A. (1994). Environmental enrichment and exploration. *Laboratory Animals*, **23**(2):38–41. II, 5.4.5

Menzel, R. and Giurfa, M. (2006). Dimensions of cognition in an insect, the honeybee. *Behavioral and Cognitive Neuroscience Reviews*, **5**(1):24–40. II

Mesulam, M. (1998). From sensation to cognition. *Brain*, **121**(6):1013–1052. 3.4.3

Mettke-Hofmann, C. (1995). Explorationsverhalten von Papageien — Adaptation an die Umwelt? *Journal fur Ornithologie*, **136**(4):468–471. II

Mettke-Hofmann, C. (2000). Changes in exploration from courtship to the breeding state in red-rumped parrots (*Psephotus haematonotus*). *Behavioural Processes*, **49**(3):139–148. II

Mettke-Hofmann, C., Rowe, K. C., Hayden, T. J., and Canoine, V. (2006). Effects of experience and object complexity on exploration in garden warblers (*Sylvia borin*). *Journal of Zoology*, **268**(4):405–413. II, 5.4.1, 5.4.2, III, III, 6.4.2

Mettke-Hofmann, C., Wink, M., Winkler, H., and Leisler, B. (2005). Exploration of environmental changes relates to lifestyle. *Behavioral Ecology*, **16**(1):247–254. II

Mettke-Hofmann, C., Winkler, H., and Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology*, **108**(3):249–272. II

Miller, N. E. and Dollard, J. (1941). *Social Learning and Imitation*. International Library of Sociology. Yale University Press, New Haven, CT. 1, III, 6.4.2, 6.4.6

Mitchinson, B., Martin, C. J., Grant, R. A., and Prescott, T. J. (2007). Feedback control in active sensing: rat exploratory whisking is modulated by environmental contact. *Proceedings of the Royal Society of London B: Biological Sciences*, **274**(1613):1035–1041. 3.4.3

Molina, M. and Jouen, F. (1998). Modulation of the palmar grasp behavior in neonates according to texture property. *Infant Behavior and Development*, **21**(4):659–666. 6.4.1, 6.4.6

Murphy, L. B. (1978). The practical problems of recognizing and measuring fear and exploration behaviour in the domestic fowl. *Animal Behaviour*, **26**(2):422–431. III

N

Nalbach, H.-O., Wolf-Oberhollenzer, F., and Kirschfeld, K. (1990). The pigeon's eye viewed through an ophthalmoscopic microscope: Orientation of retinal landmarks and significance of eye movements. *Vision Research*, **30**(4):529–540. 2.4.3, 2.4.3

Natale, L., Orabona, F., Metta, G., and Sandini, G. (2007). Sensorimotor coordination in a "baby" robot: learning about objects through grasping. In von Hofsten, C., editor, *Progress in Brain Research*, pages 403–424. Elsevier, London. 3.4.3

Necker, R. (1972). Response of trigeminal ganglion neurons to thermal stimulation of the beak in pigeons. *Journal of Comparative Physiology*, **78**(3):307–314. I, 2.2.3, 2.3.2, 4.4.2

Negro, J., Bustamante, J., Milward, J., and Bird, D. M. (1996). Captive fledgling American kestrels prefer to play with objects resembling natural prey. *Animal Behaviour*, **52**:707–714. III

Nelson, K. (2004). A welcome turn to meaning in infant development: commentary on Mandler's 'The foundations of mind: origins of conceptual thought'. *Developmental Science*, **7**(1978):506–507. 6.4.6

Nelson, M. E. M. and MacIver, M. A. M. (2006). Sensory acquisition in active sensing systems. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural and Behavioral Physiology*, **192**(6):573–586. 3.4.3

Newberry, R. C. (1995). Environmental enrichment: increasing the biological relevance of captive environments. *Applied Animal Behaviour Science*, **44**(2):22–243. II, II, 5.4.4, III

Norberg, U. M. L. (1979). Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest, and the treecreeper in relation to locomotor pattern and feeding station selection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **287**(1019):131–165. 2.4.3, 3.4

Norman, J. F., Todd, J. T., and Orban, G. A. (2004). Perception of three-dimensional shape from specular highlights, deformations of shading, and other types of visual information. *Psychological Science*, **15**(8):565–570. 6.4.1

O

Oakes, L. M., Madole, K. L., and Cohen, L. B. (2012). Infants' object examining: Habituation and categorization. *Cognitive Development*, **6**(4):377–392. 1, 6.4.6, 6.4.6, 7.4.1

O'Regan, K. and Noe, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, **24**(5):939–73; discussion 973–1031. 3.4.3

Ortega, J. and Bekoff, M. (1987). Avian play: comparative evolutionary and developmental trends. *Auk*, **104**(2):338–341. III

P

Pare, M. and Dugas, C. (1999). Developmental changes in prehension during childhood. *Experimental Brain Research*, **125**(3):239–247. 6.4.3

Parker, S. T. and Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution*, **6**(7):623–641. 3.4.3

Parron, C. and Washburn, D. (2010). Contrasting the edge- and surface-based theories of object recognition: behavioral evidence from macaques (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Behavior Processes*, **36**(1):148–157. 6.4.1

Pearson, M. J., Pipe, A. G., Melhuish, C., Mitchinson, B., and Prescott, T. J. (2007). Whiskerbot: a robotic active touch system modeled on the rat whisker sensory system. *Adaptive Behavior*, **15**(3):223–240. 6.4.4

Pellegrini, A. D. and Smith, P. K. (2004). *The Nature of Play: Great Apes and Humans*. Guilford Press, London. 5.4.1

Pellis, S. M. (1991). How motivationally distinct is play? A preliminary case study. *Animal Behaviour*, **42**(5):851–853. III

Pellis, S. M. and Iwaniuk, A. N. (2004). Evolving a playful brain: a levels of control approach. *International Journal of Comparative Psychology*, **17**(1):92–118. II

Penn, D. C., Holyoak, K. J., and Povinelli, D. J. (2008). Darwin's mistake: explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences*, **31**(2):109–178. III

Pepperberg, I. M. and Brezinsky, M. V. (1991). Acquisition of a relative class concept by an African gray parrot (*Psittacus erithacus*): discriminations based on relative size. *Journal of Comparative Psychology*, **105**(3):286–294. II

Pepperberg, I. M. and Funk, M. S. (2005). Object permanence in four species of psittacine birds: an African Grey parrot (*Psittacus erithacus*), an huger mini macaw (*Ara maracana*), a parakeet (*Melopsittacus undulatus*), and a cockatiel (*Nymphicus hollandicus*). *Animal Learning and Behavior*, **18**(1):97–108. 3.4.3, II, 6.2.1

Perone, S. S., Madole, K. L., Ross-Sheehy, S., Carey, M., and Oakes, L. M. (2008). The relation between infants' activity with objects and attention to object appearance. *Developmental Psychology*, **44**(5):1242–1248. III, 6.4.3, 6.4.6, 7.4.1

Peters, M. (1988). Footedness: asymmetries in foot preference and skill and neuropsychological assessment of foot movement. *Psychological Bulletin*, **103**(2):179–192. 4.4.2

Piaget, J. (1929). *The Child's Conception of the World*. Littlefield Adams Quality Paperbacks, London, reprint edition. 3.4.3, III, 6.4.6

Piaget, J. (1952). *The Origins of Intelligence in Children*. International Universities Press, Michigan. 3.4.3, 6.4.6

Piaget, J. (1974). *The Grasp of Consciousness: Action and Concept in the Young Child*. Routledge and Kegan Paul, London. 1, 5.4.1

Piersma, T., Aelst, R. V., Kurk, K., Berkhoudt, H., and Maas, L. R. M. (1998). A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proceedings of the Royal Society of London B: Biological Sciences*, **265**(1404):1377–1383. I, 2.4.2

Pisula, W. and Stryjek, R. (2006). Response to novelty of various types in laboratory rats. *Acta Neurobiologiae Experimentalis*, **66**:235–243. II, 5.4.3

Poti, P. and Spinozzi, G. (1994). Early sensorimotor development in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **108**(1):93–103. 3.4.3

Povinelli, D. J. (2004). Behind the ape's appearance: escaping anthropocentrism in the study of other minds. *Daedalus*, **133**(1):29–41. III

Povinelli, D. J. and Dunphy-Lelii, S. (2001). Do chimpanzees seek explanations? Preliminary comparative investigations. *Canadian Journal of Experimental Psychology*, **55**(2):185–193. 1, II, 6.4.4

Power, T. G. (2000). *Play and Exploration in Children and Animals*. Psychology Press, London, 1 edition. 1, I, 3.4.3, II, 5.4.1, III, 6.4.6, 7.4.1, C.1

Prescott, T. J., Diamond, M. E., and Wing, A. M. (2011). Active touch sensing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**(1581):2989–2995. 3.4.3

Prescott, T. J., Pearson, M., Mitchinson, B., Sullivan, J. C., and Pipe, A. G. (2009). Whisking with robots: from rat vibrissae to biomimetic technology for active touch . *IEEE Journal of Robotics and Automation*, **16**(3):42–50. 3.4.3

Preuschoft, H. (2002). What does "arboreal locomotion" mean exactly and what are the relationships between "climbing", environment and morphology? *Zeitschrift für Morphologie und Anthropologie*, **83**(2-3):171–188. 2.4.3, 3.4

Pullen, A. J., Merrill, R. J. N., and Bradshaw, J. W. S. (2012). Habituation and dishabituation during object play in kennel-housed dogs. *Animal Cognition*, **15**:1143–1150. 5.4.1

R

Raby, C. R., Alexis, D. M., Dickinson, A., and Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature*, **445**(7130):919–921. 7.4.5

Ravishankar, S., Jain, A., and Mittal, A. (2008). Multi-stage contour based detection of deformable objects. In *Computer Vision ECCV 2008*, pages 483–496. 6.4.1

Redgrave, P. P. and Gurney, K. K. (2006). The short-latency dopamine signal: a role in discovering novel actions? *Nature Reviews Neuroscience*, **7**(12):967–975. 1

Regia-Corte, T., Marchal, M., Cirio, G., and Lecuyer, A. (2012). Perceiving affordances in virtual reality: influence of person and environmental properties in perception of standing on virtual grounds. *Virtual Reality*, **17**(1):17–28. 6.4.3

Regolin, L., Marconato, F., and Vallortigara, G. (2004). Hemispheric differences in the recognition of partly occluded objects by newly hatched domestic chicks (*Gallus gallus*). *Animal Cognition*, **7**(3):162–170. 3.4.3, 3.4.3

Renner, M. J. (1988). Learning during exploration: the role of behavioral topography during exploration in determining subsequent adaptive behavior. *International Journal of Comparative Psychology*, **2**(1):43–56. II, 5.4.1

Renner, M. J. (1990). Neglected aspects of exploratory and investigatory behavior. *Psychobiology*, **18**(1):16–22. 1, 3.4.3, II, III

Renner, M. J. and Pierre, P. J. (1998). Development of exploration and investigation in the Norway Rat (*Rattus norvegicus*). *Journal of General Psychology*, **125**(3):270–291. III

Renner, M. J. and Rosenzweig, M. R. (1986). Object interactions in juvenile rats (*Rattus norvegicus*): effects of different experiential histories. *Journal of Comparative Psychology*, **100**(3):229–236. III

Renner, M. J. and Seltzer, C. P. (1991). Molar characteristics of exploratory and investigatory behavior in the rat (*Rattus norvegicus*). *Journal of Comparative Psychology*, **105**(4):326–339. 8

Renner, M. J. and Seltzer, C. P. (1994). Sequential structure in behavioral components of object investigation by Long-Evans rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, **108**(4):335. 1, III, 6.4.1, 8

Rescorla, R. A. (1968). Probability of shock in the presence and absence of CS in fear conditioning. *Journal of Comparative and Physiological Psychology*, **66**(1):1–5. 1, 3.4.3

Rheingold, H. L. (1985). Development as the acquisition of familiarity. *Annual Review of Psychology*, **36**:1–18. 1, 6.2.1, 7.4.4, 8

Rochat, P. (1987). Mouthing and grasping in neonates: evidence for the early detection of what hard or soft substances afford for action. *Infant Behavior and Development*, **10**(4):435–449. 4.4.2, III, 6.4.5

Rochat, P. (2001). *The Infant's World*. Harvard University Press, Cambridge, MA. 1, 5.4.1, 6.4.6, 6.4.6

Rodewald, A. M., Hughes, C. E., and Pitts, R. C. (2010). Development and maintenance of choice in a dynamic environment. *Journal of the Experimental Analysis of Behavior*, **94**(2):175–195. II

Rogers, L. J. (1989). Laterality in animals. *International Journal of Comparative Psychology*, **3**(1):5–25. 2.4.1, 2.4.2, 2.4.3, 3.4.3

Rogers, L. J. (1995). *The Development of Brain and Behaviour in the Chicken*. CAB International, London. 3.4.3

Rogers, L. J. (2000). Evolution of Hemispheric Specialization: Advantages and Disadvantages. *Brain and Language*, **73**(2):236–253. 3.4.3, 4.4.1, 4.4.3

Rogers, L. J. (2002). Evolution of side biases: motor versus sensory lateralization. In Mandal, M. K., Bulman-Fleming, B., and Tiwari, G., editors, *Side Bias: A Neuropsychological Perspective*, pages 3–40. Springer Netherlands, Berlin. 3.4.3, 4.4.1

Rogers, L. J. (2011). The two hemispheres of the avian brain: their differing roles in perceptual processing and the expression of behavior. *Journal of Ornithology*, **153**(S1):61–74. 4.4.3

Rogers, L. J. and Sink, H. S. (1988). Transient asymmetry in the projections of the rostral thalamus to the visual hyperstriatum of the chicken, and reversal of its direction by light exposure. *Experimental Brain Research*, **70**(2):378–384. 3.4.3, 4.4.3

Rogers, L. J., Ward, J. P., and Stafford, D. (1994). Eye dominance in the small-eared bushbaby, Otolemur garnettii. *Neuropsychologia*, **32**(2):257–264. 3.4.3, 4.4.3

Rogers, L. J., Zucca, P., and Vallortigara, G. (2004). Advantages of having a lateralized brain. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**(S6):S420–2. 4.4.3

Rosenberg, R. A. and Butler, R. A. (1982). Sound as a reinforcer for infants' manipulations of toys. *Jounral of Speech and Hearing Disorders*, **47**(3):292–295. 6.4.6

Roth, T. C., LaDage, L. D., Freas, C. A., and Pravosudov, V. (2012). Variation in memory and the hippocampus across populations from different climates: a common garden approach. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**(1727):402–410. II, 5.4.1

Roth, T. C., LaDage, L. D., and Pravosudov, V. (2010). Learning capabilities enhanced in harsh environments: a common garden approach. *Proceedings of the Royal Society of London B: Biological Sciences*, **277**(1697):3187–3193. II

Rowley, I. (1997). Family Cacatuidae (Cockatoos). In del Hoyo, J., Elliott, A., Sargatal, J., and Cabot, J., editors, *Handbook of the birds of the world, sandgrouse to cuckoos*, pages 246–269. Lynx Editions, Barcelona. I, 3.4.3, II

Rozek, Danner, Stucky, and Millam (2010). Over-sized pellets naturalize foraging time of captive Orange-winged Amazon parrots (*Amazona amazonica*). *Applied Animal Behaviour Science*, **125**(1-2):8–8. 5.4.1

Ruff, H. A. (1984). Infants' manipulative exploration of objects: Effects of age and object characteristics. *Developmental Psychology*, **20**(1):9–20. III

Ruff, H. A. (1986). Components of attention during infants' manipulative exploration. *Child Development*, **57**(1):105–114. III

Ruff, H. A. and Capozzoli, M. (2003). Development of attention and distractibility in the first 4 years of life. *Developmental Psychology*, **39**(5):877–890. 6.4.6

Ruff, H. A., Saltarelli, L. M., Capozzoli, M., and Dubiner, K. (1992). The differentiation of activity in infants' exploration of objects. *Developmental Psychology*, **28**(5):851–861. 1, 5.4.1, 6.4.2

Rusher, A. S., Cross, D. R., and Ware, A. M. (1995). Infant and toddler play: assessment of exploratory style and development level. *Early Childhood Research Quarterly*, **10**(3):297–315. 8

Rutledge and Hunt (2004). Lateralized tool use in wild New Caledonian crows. *Animal Behaviour*, **67**(2):6–6. 4.4.3

S

Sahakian, B. J., Robbins, T. W., and Iversen, S. D. (1977). The effects of isolation rearing on exploration in the rat. *Animal Learning and Behavior*, **5**(2):193–198. 5.4.1

Santana, P., Santos, C., Chainho, D., Correia, L., and Barata, J. (2010). Predicting affordances from gist. In Doncieux, S., Girard, B., Guillot, A., Hallam, J., Meyer, J.-A., and Mouret, J.-B., editors, *From Animals to Animats*, pages 325–334. Springer, Berlin. 3.4.3

Schmidt, K. A., Dall, S. R. X., and van Gils, J. A. (2009). The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos*, **119**(2):304–316. II

Schneider, T. R., Lorenz, S., Senkowski, D., and Engel, A. K. (2011). Gamma-band activity as a signature for cross-modal priming of auditory object recognition by active haptic exploration. *Journal of Neuroscience*, **31**(7):2502–2510. 3.4.3

Schrauf, C. and Call, J. (2010). Great apes use weight as a cue to find hidden food. *American Journal of Primatology*, **73**(4):323–334. 6.4.3

Schulz, L. E. (2012). The origins of inquiry: inductive inference and exploration in early childhood. *Trends in Cognitive Sciences*, **16**(7):382–389. 6.4.6, 7.4.3

Schulz, L. E. and Bonawitz, E. B. (2007). Serious fun: preschoolers engage in more exploratory play when evidence is confounded. *Developmental Psychology*, **43**(4):1045–1050. II, 6.4.3

Schulz, L. E., Kushnir, T., and Gopnik, A. (2007). Learning from doing: Intervention and causal inference. In *Causal learning: Psychology, philosophy, and computation*, pages 67–85. Oxford University Press, Oxford. 5.4.1, 6.4.6

Schulz, L. E., Standing, H. R., and Bonawitz, E. B. (2008). Word, thought, and deed: the role of object categories in children's inductive inferences and exploratory play. *Developmental Psychology*, **44**(5):1266–1276. II, III, 6.4.3, 6.4.6, 7.4.1

Sedlak, A. J. and Kurtz, S. T. (1981). A Review of Children's Use of Causal Inference Principles. *Child Development*, **52**(3):759–784. 6.4.6

Seed, A. M. and Call, J. (2008). Causal knowledge for events and objects in animals. In Okada, M., Blaisdell, A. P., and Huber, L., editors, *Rational Animals, Irrational Humans*, pages 173–188. Keio University Centre for Advanced Research on Logic and Sensibility, Logic and Informations Section, Tokyo. 1, 3.4.3

Seligman, M. E. (1970). On the generality of the laws of learning. *Psychological Review*, **77**(5):406–418. 1

Seraglia, B., Priftis, K., Cutini, S., and Gamberini, L. (2012). How tool use and arm position affect peripersonal space representation. *Cognitive Processing*, **13 Suppl 1**:325–328. II

Shettleworth, S. J. (1993). Where is the comparison in comparative cognition? Alternative research programs. *Psychological Science*, **4**(3):179–184. III

Shettleworth, S. J. (2009). The evolution of comparative cognition: is the snark still a boojum? *Behavioural Processes*, **80**(3):210–217. 5.4.4

Shettleworth, S. J. (2012). Modularity, comparative cognition and human uniqueness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1603):2794–2802. 7.4.4

Shultz, T. R. and Ravinsky, F. B. (1977). Similarity as a principle of causal inference. *Child Development*, **48**(4):1552–1558. 6.4.6

Shutts, K., Condry, K. F., Santos, L. R., and Spelke, E. S. (2009). Core knowledge and its limits: the domain of food. *Cognition*, **112**(1):120–140. III, 6.4.5

Siegler, R. S. and Liebert, R. M. (1974). Effects of contiguity, regularity, and age on children's causal inferences. *Developmental Psychology*, **10**(4):574–579. 6.4.6

Sigerson, G. (1888). Considerations of the structural and acquisitional elements in dextral pre-eminence, with conclusions as to the ambidexterity of primeval man . *Proceedings of the Royal Irish Academy*, **4**:38–50. 3.4.3, 4.4.2

Sih, A. (2011). Effects of early stress on behavioral syndromes: an integrated adaptive perspective. *Neuroscience and Biobehavioral Reviews*, **35**(7):1452–1465. II

Simpson, A. and Riggs, K. J. (2007). Under what conditions do young children have difficulty inhibiting manual actions? *Developmental Psychology*, **43**(2):417–428. 7.4.2

Simpson, A., Riggs, K. J., Beck, S. R., Gorniak, S. L., Wu, Y., Abbott, D., and Diamond, A. (2012). Refining the understanding of inhibitory processes: how response prepotency is created and overcome. *Developmental Science*, **15**(1):62–73. 7.4.2

Sloman, A. (2010). The design-based approach to the study of mind (in humans, other animals, and machines), including the study of behaviour involving mental processes. In *Proceedings of the International Symposium on AI-Inspired Biology*, pages 87–94. 7.4.4

Sloman, S. (2009). *Causal Models: How People Think About the World and Its Alternatives*. Oxford University Press, USA. 6.4.6

Smith, A. M., Chapman, C. E., Donati, F., Fortier-Poisson, P., and Hayward, V. (2009). Perception of simulated local shapes using active and passive touch. *Journal of Neurophysiology*, **102**(6):3519–3529. 3.4.3

Smith, G. A. (1971). The use of the foot in feeding, with especial reference to parrots. *Avicultural Magazine*, **77**:93–100. 3.4.3, 4.4.2, 4.4.3

Smith, G. A. (1975). Systematics of Parrots. *Ibis*, **117**(1):18–68. 3.4.3, II, 5.4.1, III, III

Snyder, P. J. and Bonner, J. A. (2001). Postnatal development of lateralized motor preference in the African grey parrot (*Psittacus erithacus*). *Brain and Cognition*, **46**(1-2):276–279. 3.4.3, 3.4.3, 4.4.3

Snyder, P. J. and Harris, L. J. (1997). Lexicon size and its relation to foot preference in the African grey parrot (*Psittacus erithacus*). *Neuropsychologia*, **35**(6):919–926. 2.4.1, 2.4.2, 2.4.3, 3.4.3, 3.4.3, 3.4.3, 4.4.3

Sobel, D. M., Tenenbaum, J. B., and Gopnik, A. (2004). Children's causal inferences from indirect evidence: backwards blocking and Bayesian reasoning in preschoolers. *Cognitive Science*, **28**(3):303–333. 6.4.6

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., and Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences*, **102**(15):5460–5465. II

Sol, D., Griffin, A. S., Bartomeus, I., and Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PloS One*, **6**(5):e19535. 5.4.2

Soto, F. A. and Wasserman, E. A. (2012). Visual object categorization in birds and primates: integrating behavioral, neurobiological, and computational evidence within a "general process" framework. *Cognitive, Affective and Behavioral Neuroscience*, **12**(1):220–240. III, 6.4.1, 6.4.5

Sparks, J. and Soper, T. (1990). *Parrots: A Natural History*. Facts on File Inc., New York. 2.4.3

Spelke, E. S. (2000). Core knowledge. *American Psychologist*, **55**(11):1233–1243. 1, 6.4.6, 6.4.6, 6.4.6, 7.4.2

Spelke, E. S. (2003). What makes us smart? Core knowledge and natural language. In Gentner, D., editor, *Language in Mind: Advances in the Study of Language and Thought*, pages 277–311. MIT Press, Boston. 7.4.2

Spelke, E. S., Lee, S.-A., and Izard, V. (2010). Beyond core knowledge: natural geometry. *Cognitive Science*, **34**(5):863–884. 6.4.1

Spoon, T. R., Millam, J. R., and Owings, D. H. (2004). Variation in the stability of cockatiel (*Nymphicus hollandicus*) pair relationships: the roles of males, females, and mate compatibility. *Behaviour*, **141**:1211–1234. II

Srinivasan, M. and Gregory, R. L. (1992). How Bees Exploit Optic Flow: Behavioural Experiments and Neural Models [and Discussion]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **337**(1281):253–259. II

Stahl, L. and Pry, R. (2005). Attentional flexibility and perseveration: developmental aspects in young children. *Child Neuropsychology*, **11**(2):175–189. 7.4.3

Sterelny, K. (2007). Social intelligence, human intelligence and niche construction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**(1480):719–730. II

Stingelin, W. (1965). Qualitative and quantitative studies of the nuclear regions of the medulla oblongata in birds. *Bibliotheca anatomica*, **6**:1–116. I, 3.4.3, 4.4.2

Storli, R. and Hagen, T. L. (2010). Affordances in outdoor environments and children's physically active play in pre-school. *European Early Childhood Education Research Journal*, **18**(4):445–456. II

Streri and Feron (2005). The development of haptic abilities in very young infants: From perception to cognition. *Infant Behavior and Development*, **28**(3):15–15. 4.4.2

Sultan, F. F. (2005). Why some bird brains are larger than others. *Current Biology*, **15**(17):R649–R650. I, 3.4.3, 4.4.2

Sumowski, J. F., Wylie, G. R., DeLuca, J., and Chiaravalloti, N. (2010). Intellectual enrichment is linked to cerebral efficiency in multiple sclerosis: functional magnetic resonance imaging evidence for cognitive reserve. *Brain*, **133**(2):362–374. II

Sussman, G. J. (1973). *A Computational Model of Skill Acquisition*. PhD thesis, Elsevier Science Inc., Boston. 1

Switzky, H. N., Haywood, H. C., and Isett, R. (1974). Exploration, curiosity, and play in young children: effects of stimulus complexity. *Developmental Psychology*, **10**(3):321–329. III, 6.4.2, 6.4.6

Switzky, H. N., Ludwig, L., and Haywood, H. C. (1979). Exploration and play in retarded and nonretarded preschool children: effects of object complexity and age. *American Journal of Mental Deficiency*, **83**(6):637–644. 1, 6.4.2

T

Taylor, A. H., Hunt, G. R., Medina, F. S., and Gray, R. D. (2009a). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society of London B: Biological Sciences*, **276**(1655):247–254. 1

Taylor, A. H., Medina, F. S., Holzhaider, J. C., Hearne, L. J., Hunt, G. R., and Gray, R. D. (2010). An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. *PloS One*, **5**(2):e9345. 7.4.2

Taylor, A. H., Roberts, R., Hunt, G. R., and Gray, R. D. (2009b). Causal reasoning in New Caledonian crows: Ruling out spatial analogies and sampling error. *Communicative and Integrative Biology*, **2**(1942-0889):311–312. III

Taylor, L. J. and Zwaan, R. A. (2010). Grasping spheres, not planets. *Cognition*, **115**(1):39–45. III, 6.4.1

Tebbich, S., Sterelny, K., and Teschke, I. (2010). The tale of the finch: adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**(1543):1099–1109. II

Tecwyn, E. C., Thorpe, S. K. S., and Chappell, J. (2012). What cognitive strategies do orangutans (*Pongo pygmaeus*) use to solve a trial-unique puzzle-tube task incorporating multiple obstacles? *Animal Cognition*, **15**(1):121–133. III, 6.4.5

Tenenbaum, J. B. (1999). *A Bayesian framework for concept learning*. PhD thesis, Citeseer, London. 1

Tenenbaum, J. B., Griffiths, T. L., and Kemp, C. (2006). Theory-based Bayesian models of inductive learning and reasoning. *Trends in Cognitive Sciences*, **10**(7):309–318. 1, 6.4.6

Teschner, M., Heidelberger, B., Muller, M., and Gross, M. (2004). A versatile and robust model for geometrically complex deformable solids. *Computer Graphics*, **4**:312–319. 6.4.5

Teyke, T. (1988). Flow field, swimming velocity and boundary layer: parameters which affect the stimulus for the lateral line organ in blind fish. *Journal of Comparative Physiology*, **163**(1):53–61. 3.4.3

Thomas, R. K. (1996). Investigating cognitive abilities in animals: unrealized potential. *Cognitive Brain Research*, **3**(3-4):157–166. III

Thornton, A. and Lukas, D. D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**(1603):2773–2783. 8

Thorpe, S. K. S., Crompton, R. H., and Alexander, R. M. (2007a). Orangutans use compliant branches to lower the energetic cost of locomotion. *Biology Letters*, **3**(3):253–256. 6.4.5

Thorpe, S. K. S., Holder, R. L., and Crompton, R. H. (2007b). Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science*, **316**(5829):1328–1331. 2.4.3, 3.4

Toates, F. M. (1983). Exploration as a motivational and learning system: a cognitive incentive view. In Archer, J. and Birke, L. I. A., editors, *Exploration in animals and humans*, pages 55–71. Van Nostrand Reinhold, Berkshire, England. 1

Tobalske, B. W. (2004). Take-off mechanics in hummingbirds (Trochilidae). *Journal of Experimental Biology*, **207**(8):1345–1352. 2.4.3, 3.4

Tobalske, B. W. (2007). Biomechanics of bird flight. *Journal of Experimental Biology*, **210**(18):3135–3146. 2.4.3, 3.4

Tokita, M. (2004). Morphogenesis of parrot jaw muscles: understanding the development of an evolutionary novelty. *Journal of Morphology*, **259**(1):69–81. I, 3.4.3

Tokita, M., Kiyoshi, T., and Armstrong, K. N. (2007). Evolution of craniofacial novelty in parrots through developmental modularity and heterochrony. *Evolution and Development*, **9**(6):590–601. I

Tolman, E. and Krechevsky, I. (1933). Means-end-readiness and hypothesis–A contribution to comparative psychology. *Psychological Review*, **40**(1):60–70. 1

Tomonaga, M. (1998). Perception of shape from shading in chimpanzees (Pan troglodytes) and humans (Homo sapiens). *Animal Cognition*, **1**(1):25–35. 6.4.1

Troscianko, J., von Bayern, A. M. P., Chappell, J., Rutz, C., and Martin, G. R. (2012). Extreme binocular vision and a straight bill facilitate tool use in New Caledonian crows. *Nature Communications*, **3**:1110–1110. 3.4.3

Turvey, M. T. (1996). Dynamic touch. *American Psychologist*, **51**(11):1134–1152. 6.4.6

Turvey, M. T. and Carello, C. (2011). Obtaining information by dynamic (effortful) touching. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**(1581):3123–3132. 1, 3.4.3, 6.4.6

U

Ulanovsky, N. and Moss, C. J. (2007). Hippocampal cellular and network activity in freely moving echolocating bats. *Nature Neuroscience*, **10**(2):224–233. 3.4.3

Uzgiris, I. and Hunt, J. (1989). *Assessment in Infancy: Ordinal Scales of Psychological Development*. University of Illinois Press, Chicago, IL. 6.2.4, 6.2.2

V

Vallortigara, G. and Andrew, R. J. (1994). Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behavioural Processes*, **33**(1–2):41–57. 3.4.3, 3.4.3

van Hoek, C. S. and ten Cate, C. (1998). Abnormal behavior in caged birds kept as pets. *Journal of Applied Animal Welfare Science*, **1**(1):51–64. II, 5.4.1, 5.4.4

van Schaik, C. P., Deaner, R. O., and Merrill, M. Y. (1999). The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, **36**(6):719–741. III

Vandenberg, B. (1984). Developmental features of exploration. *Developmental Psychology*, **20**(1):3–8. 6.4.6, 7.4.4

Varty, G. B., Paulus, M. P., Braff, D. L., and Geyer, M. A. (2000). Environmental enrichment and isolation rearing in the rat: effects on locomotor behavior and startle response plasticity. *Biological Psychiatry*, **47**(10):864–873. 5.4.1

Verbeek, M. E., Drent, P. J., and Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, **48**(5):1113–1121. III

Vestergaard, K. (1982). Dust-bathing in the domestic fowl—diurnal rhythm and dust deprivation. *Applied Animal Ethology*, **8**(5):487–495. 5.4.1

Visalberghi, E. and Neel, C. (2003). Tufted Capuchins (*Cebus apella*) use weight and sound to choose between full and empty nuts. *Ecological Psychology*, **15**(3):215–228. III, III, 6.4.3

Visalberghi, E. and Tomasello, M. (1998). Primate causal understanding in the physical and psychological domains. *Behavioural Processes*, **42**(2-3):189–203. 1

Vlamings, P. H. J. M., Hare, B., and Call, J. (2010). Reaching around barriers: the performance of the great apes and 3-5-year-old children. *Animal Cognition*, **13**(2):273–285. 7.4.2

von Bayern, A. M. P., Heathcote, R. J., Rutz, C., and Kacelnik, A. (2009). The role of experience in problem solving and innovative tool use in crows. *Current Biology*, **19**(22):1965–1968. II, 7.4.4

von Hofsten, C. and Rosander, K. (2007). *From Action to Cognition*. Elsevier, London. 3.4.3

Voss, J. and Bischof, H. J. (2009). Eye movements of laterally eyed birds are not independent. *Journal of Experimental Biology*, **212**(10):1568–1575. 2.4.3, 3.4.3, 4.4.1, 8

W

Warburton, K. and Hughes, R. (2011). Learning of Foraging Skills by Fish. pages 10–35. Wiley-Blackwell, Oxford, UK. II

Warhol, A. and Benirschke, K. (1986). Puerto Rican Parrot. In *Vanishing Animals*, pages 94–98. Springer, New York, NY. 2.4.3

Warren Jr, W. (1998). Visually controlled locomotion: 40 years later. *Ecological Psychology*, **10**(3-4):177–219. 2.4.3

Warrick, D. R., Bundle, M. W., and Dial, K. P. (2002). Bird maneuvering flight: blurred bodies, clear heads. *Integrative and Comparative Biology*, **42**(1):141–148. 2.4.3, 3.4, 3.4.2

Wasserman, E. A., Castro, L., and Freeman, J. H. (2012). Same-different categorization in rats. *Learning and Memory*, **19**(4):142–145. III, 6.4.5

Webb, N. V., Famula, T. R., and Millam, J. R. (2010). The effect of rope color, size and fray on environmental enrichment device interaction in male and female Orange-winged Amazon parrots (*Amazona amazonica*). *Applied Animal Behaviour Science*, **124**(3-4):149–156. II, 5.4.3

Webb, R. (2000). Stella: Polyhedron Navigator. *Symmetry: Culture and Science*, **11**(1-4):231–268. 6.2.3

Weir, A. A. S. A., Kenward, B. B., Chappell, J., and Kacelnik, A. A. (2004). Lateralization of tool use in New Caledonian crows (Corvus moneduloides). *Proceedings of the Royal Society of London B: Biological Sciences*, **271 Suppl 5**:S344–S346. 3.4.3, 4.4.3

Weisler, A. and McCall, R. B. (1976). Exploration and play: resume and redirection. *American Psychologist*, **31**(7):492–508. III

Weissert, R. and Campenhausen, C. (1981). Discrimination between stationary objects by the blind cave fishAnoptichthys jordani (Characidae). *Journal of Comparative Physiology*, **143**(3):375–381. 3.4.3

Welder, A. N. and Graham, S. A. (2001). The influence of shape similarity and shared labels on infants' inductive inferences about nonobvious object properties. *Child Development*, **72**(6):1653–1673. 6.4.6

Wemelsfelder, F. and Birke, L. I. A. (1997). Environmental challenge. In Appleby, M. C. and Hughes, B. O., editors, *Animal Welfare*, pages 65–95. CAB International, Wallingford. 1

Westerskov, K. (1981). Reishek's 1898 paper on 'The kakapo (*Strigops habroptilus*) in the wild and in captivity'. *Nortornis*, **28**(4):263–280. 2.4.3

White, R. W. (1959). Motivation reconsidered: The concept of competence. *Psychological Review*, **66**(5):297–333. 6.4.6

Whittow, G. C. and Sturkie, P. D. (1999). *Sturkie's Avian Physiology*. Academic Press, New York. I, 2.4.1, 3.4.3, 4.4.1

Wild, J. M. (1981). Identification and localization of the motor nuclei and sensory projections of the glossopharyngeal, vagus, and hypoglossal nerves of the cockatoo (*Cacatua roseicapilla*), Cacatuidae. *Journal of Comparative Neurology*, **203**(3):351–377. I, 3.4.3, 4.4.2

Wild, J. M., Reinke, H., and Farabaugh, S. M. (1997). A non-thalamic pathway contributes to a whole body map in the brain of the budgerigar. *Brain Research*, **755**(1):137–141. I, 3.4.3, 4.4.2

Williams, E. H. and Bunkley-Williams, L. (2012). Rapid beak-swinging locomotion in the Puerto Rican Spindalis. *Wilson Journal of Ornithology*, **118**(4):571–572. 2.4.3, 3.4.1

Williams, L. (1978). Casting curved shadows on curved surfaces. In *ACM SIGGRAPH Computer Graphics*, pages 270–274, New York. ACM. 6.4.1

Wilz, K. J. and Bolton, R. L. (1971). Exploratory behavior in response to the spatial rearrangement of familiar stimuli. *Psychonomic Science*, **24**(3):117–118. II

Winefield, A. H., Green, A., and Metzer, J. C. (2002). Perceptual learning in the rat: stimulus differentiation or latent inhibition of common elements? *Journal of General Psychology*, **129**(2):170–180. 2.4.3

Wing, A. M. and Lederman, S. J. (1998). Anticipating load torques produced by voluntary movements. *Journal of Experimental Psychology: Human Perception and Performance*, **24**(6):1571–1581. 6.4.3, 6.4.4

Wing, A. M. and Lederman, S. J. (2009). Points for precision grip. In Nowak, D. A. and Hermsdorfer, J., editors, *Sensorimotor Control of Grasping: Physiology and Pathophysiology STROKE*, pages 193–203. Cambridge University Press, Cambridge. 4.4.2, 6.4.1

Withagen, Araujo, and Pepping (2012). Affordances can invite behavior: Reconsidering the relationship between affordances and agency. *New Ideas in Psychology*, **30**(2):9–9. 7.4.2

Witmer, L. M., Chatterjee, S., Franzosa, J., and Rowe, T. (2003). Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. *Nature*, **425**(6961):950–953. 2.4.3

Wood-Gush, D. G. M. and Vestergaard, K. (1991). The seeking of novelty and its relation to play. *Animal Behaviour*, **42**(4):599–606. II, 5.4.3, III, III, 6.4.3

Wood-Gush, D. G. M., Vestergaard, K., and Volker Petersen, H. (1990). The significance of motivation and environment in the development of exploration in pigs. *Biology of Behaviour*, **15**(1):39–52. II, 5.4.4

X

Xu, F. (2011). Categorization, object individuation, and object manipulation: Commentary on "Object manipulation facilitates kind-based object individuation of shape-similar objects" by O.S. Kingo and P. Krøjgaard (2011). *Cognitive Development*, **26**(2):104–105. III, 6.4.5

Y

Yoo, J. H. (2009). Uncertainty reduction and information valence: Tests of Uncertainty Reduction Theory, Predicted Outcome Value, and an alternative explanation. *Human Communication*, **12**(2):187–198. II

Z

Zeffer, A. and Norberg, U. M. L. (2003). Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion. *Journal of Experimental Biology*, **206**(Pt 6):1085–1097. 2.4.3, 3.4, 3.4.1

Zhang, W., Gordon, A. M., Fu, Q., and Santello, M. (2010). Manipulation after object rotation reveals independent sensorimotor memory representations of digit positions and forces. *Journal of Neurophysiology*, **103**(6):2953–2964. III, 6.4.4

Zhu, Q. and Bingham, G. P. (2010). Learning to perceive the affordance for long-distance throwing: smart mechanism or function learning? *Journal of Experimental Psychology: Human Perception and Performance*, **36**(4):862–875. 6.4.3

Zimmerman, C. (2007). The development of scientific thinking skills in elementary and middle school. *Developmental Review*, **27**(2):172–223. 6.4.6

Zimmermann, A., Stauffacher, M., Langhans, W., and Wurbel, H. (2001). Enrichment-dependent differences in novelty exploration in rats can be explained by habituation. *Behavioural Brain Research*, **121**(1-2):11–20. 6.4.2

Zweers, G. A. and Berkhoudt, H. (1994). Behavioral mechanisms of avian feeding. *Advances in Comparative and Environmental Physiology*, **18**:243–279. I, 3.4.3